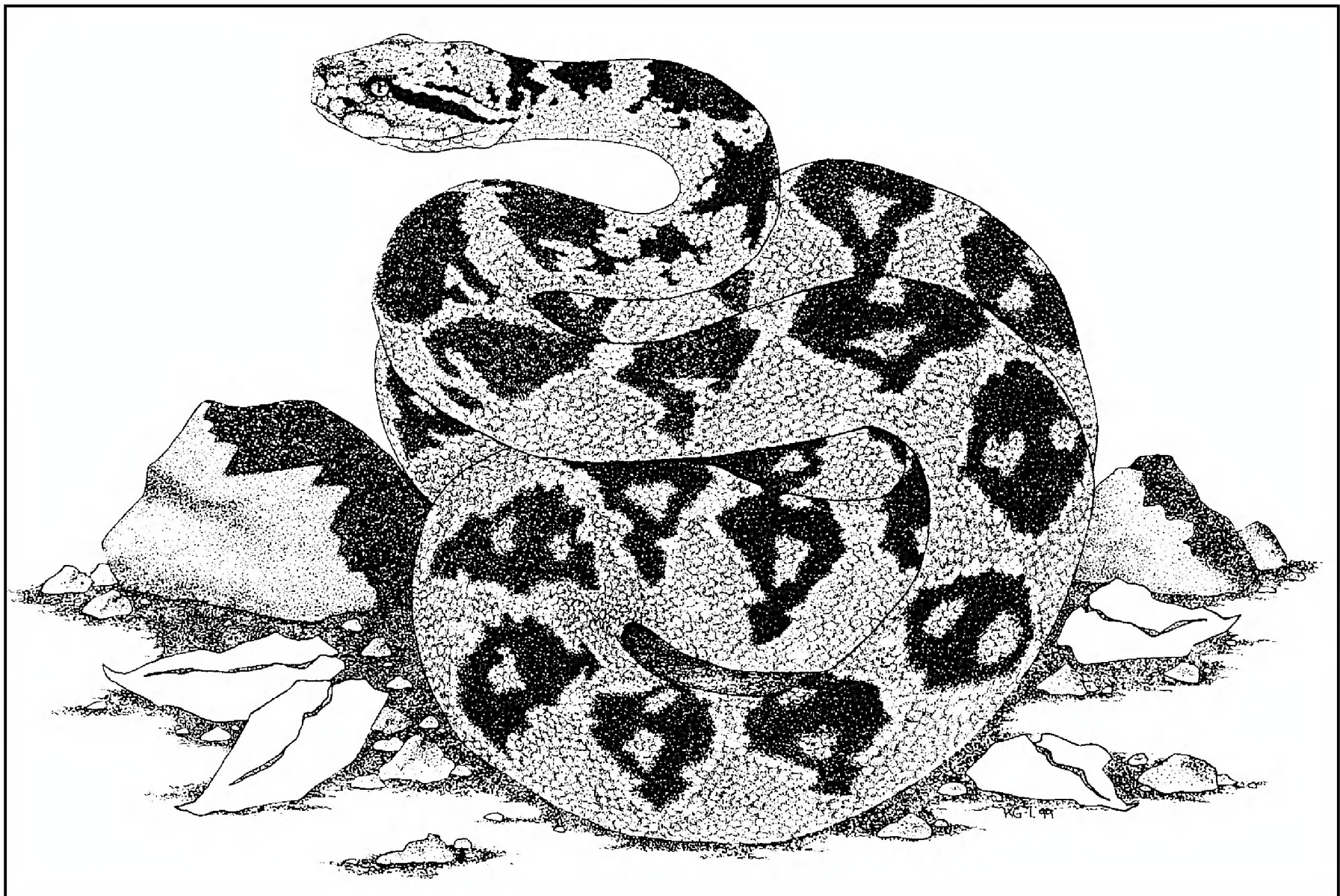

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BULLETIN OF THE CHICAGO HERPETOLOGICAL SOCIETY

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Keys to Understanding the Bushmasters (Genus *Lachesis* Daudin, 1803)

Dean Ripa*
Ripa Ecologica, S.A.
Punta Uva
Costa Rica

Introduction

Through my involvement with bushmasters, and my attempts to devise a workable systematics for these snakes that need not resort to geographic guidelines for identification purposes, I came to realize the need for a comprehensive work that would allow the researcher to understand the complex morphological variations within this unique genus of snakes. In Ripa (1994), I presented morphological differences between the Central and South American groups that indicated an abandonment of the longstanding polytypic classification, introducing the idea that the bushmasters were not one species but three (one species, *Lachesis muta*, having two subspecies). The tables at the end of the present article allow visual comparisons to be made among these three great pitvipers: *L. muta* (Linnaeus, 1766); *L. stenophrys* Cope, 1876; and *L. melanocephala* Solórzano and Cerdas, 1986. This can only build a stronger case for their recent treatment by Zamudio and Greene (1997) as three distinct species.

I also hope that the comparative data generated will help solve the continuing enigma of the affinity of the bushmaster of eastern Panama, northwestern Colombia and Ecuador, and the inter-Andean valleys of Colombia. This form is presently in taxonomic limbo. In the older literature it is called *L. muta* on the basis of high ventral scale count, head markings and distribution within mainland South America (Hoge and Romano-Hoge, 1981; Martínez and Bolaños, 1982). In more recent writings it has been placed with *L. stenophrys* on the basis of an apparently continuous distribution with the latter species in Central America (Campbell and Lamar, 1989; Ripa, 1994; Zamudio and Greene, 1997). While all agree to the controversial status of this form, in no case has a comparative systematic examination of this population been made. Ripa (in prep.) takes the first comprehensive look at this unresolved taxon, revealing it more closely related to the Amazonian South American lineages than to *L. stenophrys*. However, significant differences from both South American and Central American forms indicate that this population does not belong to either group; rather it represents a widespread, distinct and allopatric population that has been separated from the two other bushmaster species for millions of years. The bushmaster of eastern Panama-northwestern South America meets the definition of a distinct evolutionary species, as a "single lineage of ancestral descendant populations of organisms which maintains its identity from other such lineages and which has its own evolutionary tendencies and historical fate" (Wiley, 1978; modified from Simpson, 1961). Herein called "Darien bushmaster" pending description as a new species (Ripa, in prep.), this bushmaster has been given its own deserved column in the tables. A range map is provided to show the distribution of this form with

respect to a revised distribution range for *L. stenophrys*.

Readers interested in investigating this phenomenon further are referred to the above-mentioned Ripa (in prep.) article.

Of great interest also are the life habits of bushmasters, which show special differences from other snakes. So, along with the section on morphology I have provided notes on behavioral, predatory and reproductive characteristics, also presented in the format of tables. A comparative look at bushmasters vis-à-vis a coexistent pitviper, the terciopelo (*Bothrops asper*), is also included.

Materials and Methods

Materials are vouchered specimens from the following museums and institutions: American Museum of Natural History (AMNH); Instituto Butantan, São Paulo, Brazil (I.B.); Zoological Museum of the School of Biology, University of Costa Rica (USC-CR); Gorgas Memorial Laboratory, Panama (GML); Museum of Comparative Zoology at Harvard, Cambridge (MCZ); University of Kansas Museum of Natural History (KUMNH); University of North Carolina at Wilmington (UNCW); and United States National Museum, Smithsonian Institution, Washington (USNM).

Species and number of specimens were: *Lachesis muta*, 50 (including *L. muta rhombeata*); *L. stenophrys*, 40; and *L. melanocephala*, 25. Mature adult specimens having an approx. total length of 2 m were used. Additional groups of neonates and juveniles were used where applicable.

For the "Darien bushmaster" (of eastern Panama-northwestern Colombia and Ecuador) there were a total of 17 vouchered museum specimens of various age/size groups. But some specimens were incomplete: There were six "whole" 2 m adults; and three whole juveniles of just over 1 m length. There were two adult "heads" that retained full body skin with intact whole tails (total length approx. 2 m). There were four other adult heads without attached skins. There was a head from a snake estimated to have been five or six months of age. The remaining specimen was an adult full body skeleton. One of the adult specimens (USC-CR 8061) appears to have starved to death in captivity, and despite its length, did not appear to be a mature adult, so it was not used in the body weight and related measurements. This accounts for the variation in sample sizes for these snakes in the tables.

The following specimens of the "Darien bushmaster" were examined: AMNH-R 18243, Atrato region, Colombia; AMNH-R 107656, Quebrada Docordo, Choco, Colombia; AMNH-R 107921, Quebrada Guanguí (Rio Patia), Cauca, Colombia; AMNH-R 109641, Altos de Maje, Panamá;

* Mailing address: 4608 Cedar Avenue, Wilmington, NC 28403. E-mail: <DMRipa@aol.com>.



Figure 1. Relative girths of bushmasters: South American *L. muta* (upper); Central American *L. stenophrys* (lower). The *L. muta* is of greater total length (230 cm) and age (6 yrs); the *L. stenophrys* is 200 cm and weighs nearly twice the *L. muta*, with greater midbody height. *L. muta* has a rounder body conformation, while *L. stenophrys* has a taller, more laterally compressed body conformation, one of numerous characteristics that differentiate these species.



Figure 2. (Lower) *Lachesis stenophrys*. (Upper) *Lachesis* sp. (MCZ 29253) from Choco, Colombia, that has been called both *L. stenophrys* and *L. muta* in the literature.



Figure 3. (Right) *Lachesis stenophrys*. (Left) *Lachesis* sp. from Choco, Colombia. Note the "arabesque" head markings, and extremely rugose scalation in the latter form. In *L. stenophrys*, among numerous other differences, the head markings are usually absent or minimal when occurring.



Figure 4. Heads of South American bushmasters, *L. m. muta* (left and center), and head of "Darien bushmaster" (right). The author believes this form to be a distinct species, more closely related to the South American lineage than to Central American *L. stenophrys*.

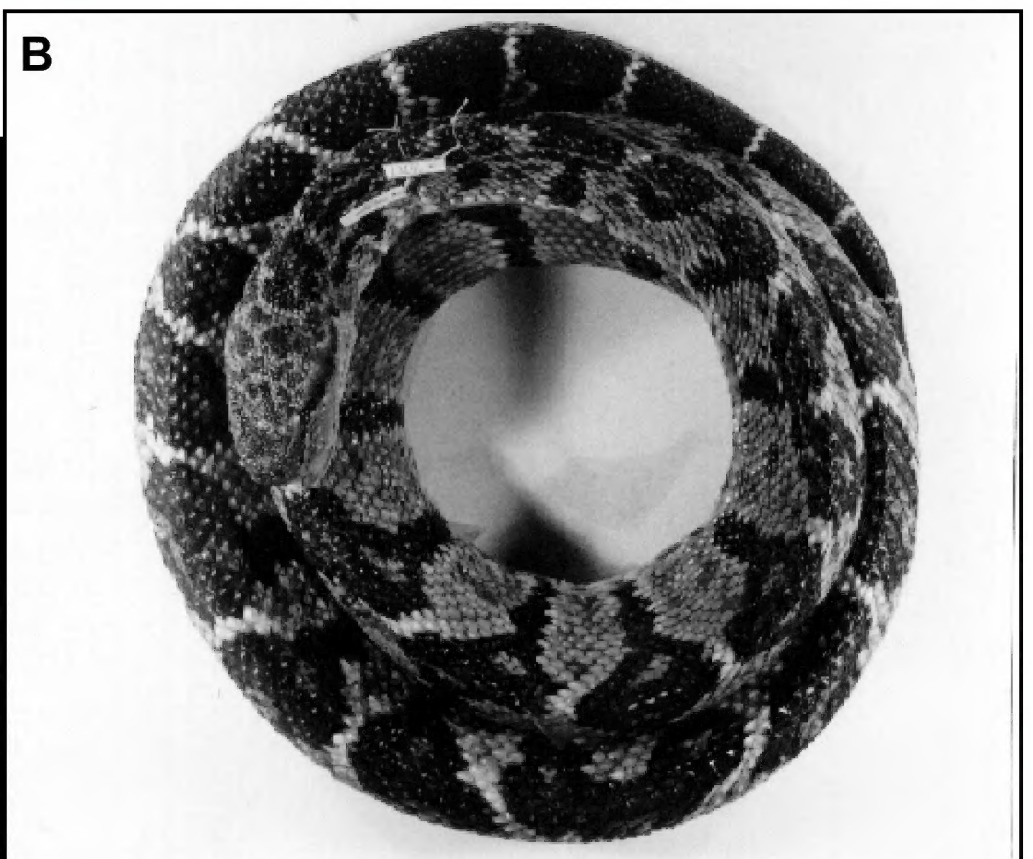


Figure 5. KUMNH 75767, Laguna, Serrania del Darien, Darien, Panama. The "mystery" bushmaster from eastern Panama. Cross the dry forest barriers of the Chepo region in eastern Panama and the bushmaster changes into a strikingly different animal that so perplexed Martínez and Bolaños (1982) that they called it *L. [muta] muta* and gave eastern Panama as a range extension for that species [then subspecies]. Campbell and Lamar (1989) reported it as *L. stenophrys* based on geographic grounds. While sharing some traits with the Central American forms, this snake is morphologically closer to South American *L. m. muta*. **A.** Head. **B.** Dorsal view of entire specimen.

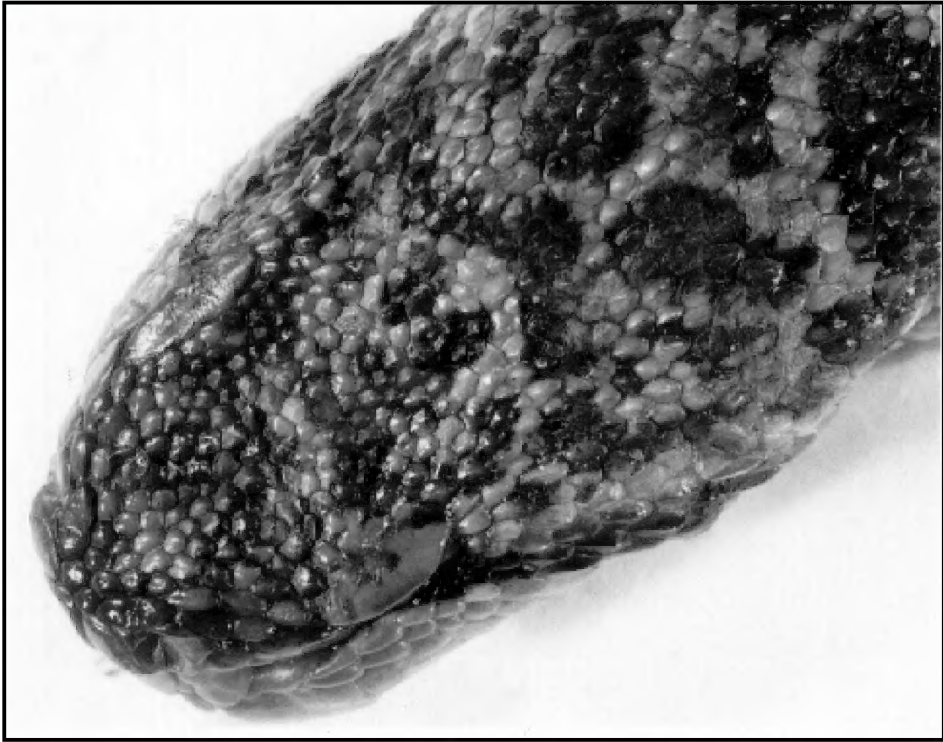


Figure 6. Dorsal head markings of the eastern Panamanian form, echoing trends seen in *L. muta rhombeata* and *L. muta muta* from Mato Grosso area of Brazil. Head markings in bushmasters (including the full black head dorsum of *L. melanocephala*) may be associated with high elevation and lower rainfall, probably due to increased UV exposure. In eastern Panama, this form inhabits areas of lower rainfall than other bushmasters, and has been taken from elevations above 1100 m.



Figure 7. AMNH-R 109641 Head of a "Darien bushmaster." Alto de Maje, eastern Panama, near the border of Darien, Panama province. Collected by C. W. Myers in 1972.

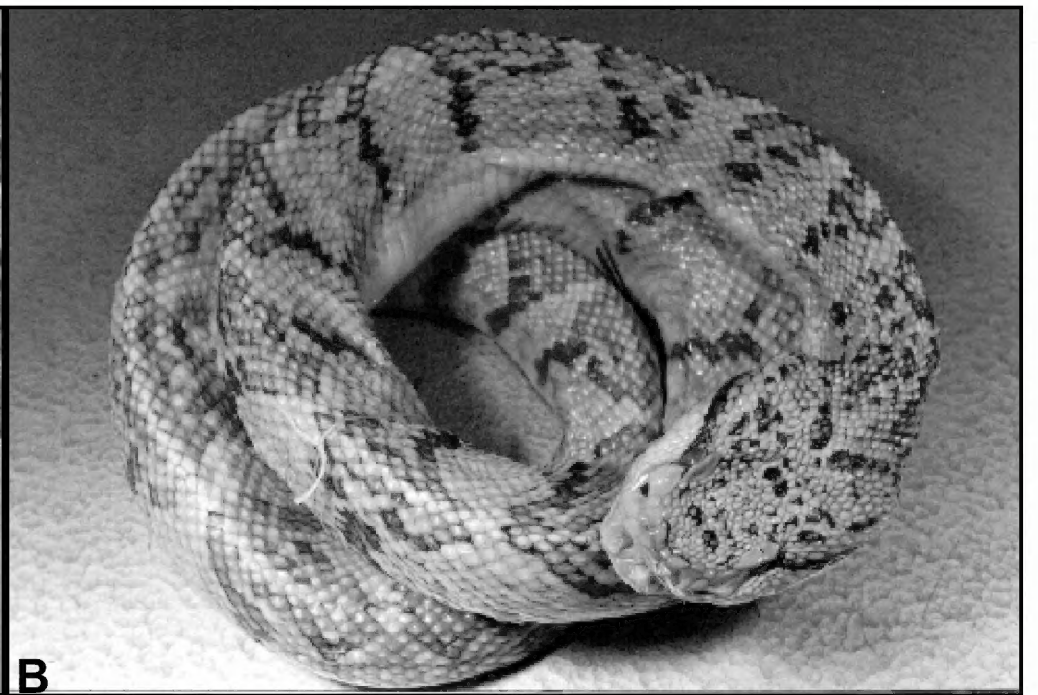
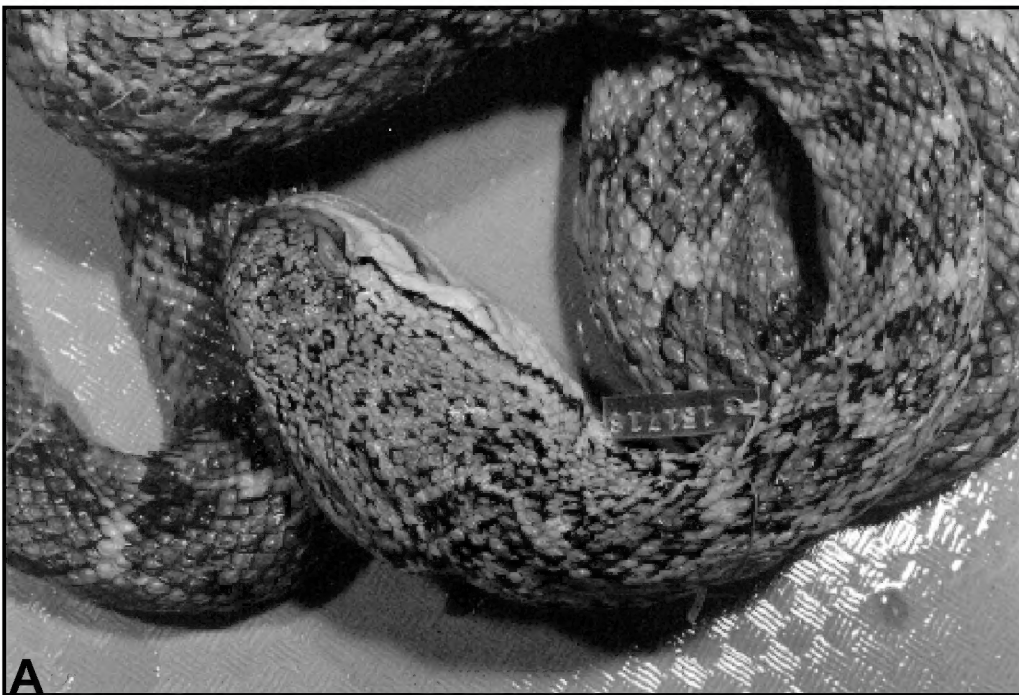


Figure 8. A. USNM 151716, Rio Raposo, near Buenaventura, Cauca, Colombia. 1.2 m, juvenile. "Darien bushmaster." B. AMNH-R 18243, Atrato Region, Colombia. Neonate. An example of "Darien bushmaster" from the Caribbean lowlands of northern Colombia.

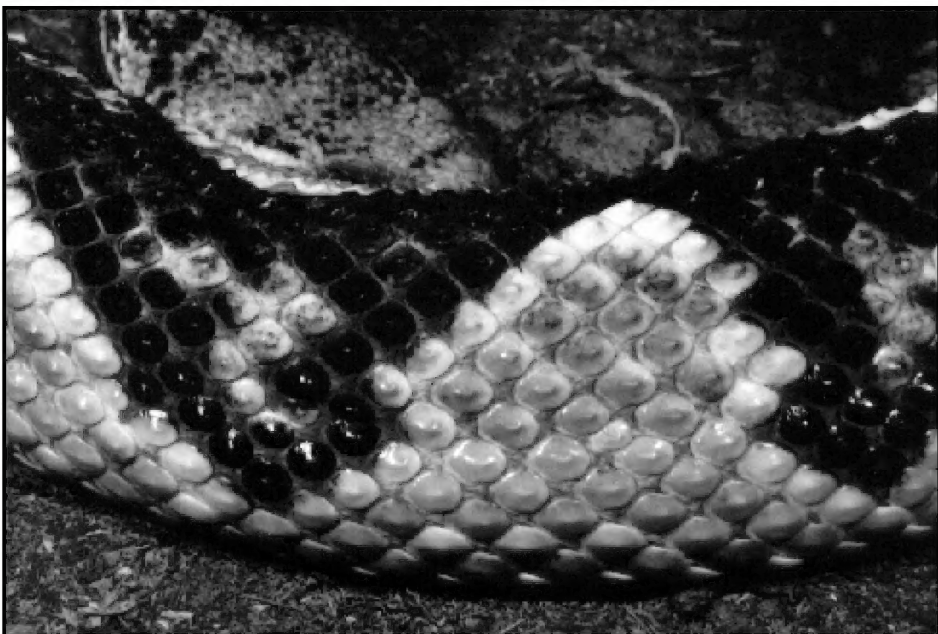


Figure 9. Dorsolateral scalation of *L. muta muta*, showing the large, beaded, diamond-shaped dorsolateral midbody scales of the bushmasters of the Guiana Shield. There is little or no free apex; the basal portion is V- or U-shaped at the point of emergence from the interstitial skin. Pattern is usually rhomboidal.

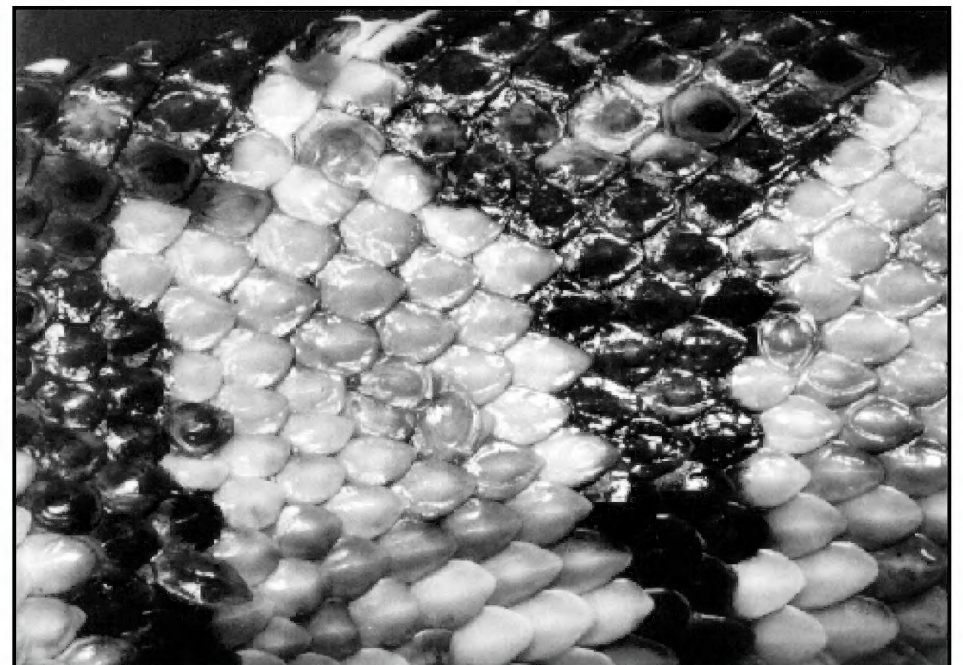


Figure 10. This eastern Panamanian example shows a dorsolateral midbody scalation similar to the two Central American forms: Flat, imbricate, and a blunt basal end, and obtuse keeling dorsolaterally that tends away from the midline of the scale and may reach the free apical portion. The dorsal pattern tends to vertical bars, which may reach the ventrals.

AMNH-R 109813 Quebrada Guanguí (Rio Patia), Cauca, Colombia; KUMNH 75767, Laguna, Darién, Panamá; KUMNH 117479, Cerro Cituro, Serranía de Pirre, Darién, Panamá; MCZ 32444, Boca de Cupe, Darién, Panamá; MCZ 37138, Yavisa, Darién, Panamá; MCZ 29253, Choco, Colombia; USC-CR 8061, Playa Chuzo, Darién, Panamá; USNM 020635, Esmeraldas, Ecuador; USNM 151714, Valle del Cauca, Colombia; USNM 151715, Valle del Cauca, Colombia; USNM 151716, Valle del Cauca, Colombia; USNM 165008, Esmeraldas, Ecuador; USNM 237086, Esmeraldas, Ecuador.

Measurements were taken to the nearest millimeter, using a ruler and a calipers accurate to 1 mm. To enhance physical examination and detail I have used macrophotography, and in osteological references, radiographs.

A note on behavioral observations: Source materials were 54 wild-caught snakes, collected individually or by use of the “bounty system” while in the countries of Brazil, Guyana, Surinam, Costa Rica and Panamá, over a 15-year period. Captive-reproduced progeny from this group were also used, totaling 150+ specimens. (For a summary of some of the methods I have used to reproduce bushmasters in captivity, see Ripa [1994].) Field observations formed another source of data, however limited. The difficulty of finding bushmasters in natural habitat is compounded by the equally difficult conditions with which the field worker must cope. Bushmasters are secretive, nervous snakes, and one has only those few moments before the snake becomes alerted to the observer’s presence, and ceases being a good (or available) subject. The promising area of radiotelemetry, which works for many snakes, does not seem viable for bushmasters owing to what would appear to be a unusually delicate constitution for a large viper: the radio-tagged snake rarely behaves normally after the implantation, reverting to the syndrome long ago described by Ditmars after these animals had been force-fed, becoming “sluggish, benumbed, and rarely crawling.” In consideration of these problems, and because field observations can rarely if ever be



Figure 11. USNM 154086, Rio Batovi, Alto Rio Xingo. The “Mato Grosso” bushmaster is one of two variable forms of *L. muta*, occupying the east Andean versants from northeastern Colombia south through Ecuador, eastern Peru and northeastern Bolivia, east into Brazil’s Mato Grosso region. It is nearly indistinguishable from *L. muta rhombeata* of Brazil’s Atlantic Forest. Arabesque head markings characterize this form. In parts of the eastern Andes the head markings may be so elaborate as to make the head dorsum almost completely black.

repeated, I have turned to the captive environment as a more reliable means of study. Not only can environmental conditions be simulated, but one can manipulate those conditions in order to replicate behavior. The enclosures used at my facility mimic insofar as is possible the temperature, humidity and photogradients derived from my field observations of natural habitat; they are spacious (up to 45 m²) and can be modified in size according to the necessities of the experiment. Since bushmasters are largely nocturnal, most observation is conducted during their natural active cycle. A total of over 15,000 observation hours have gone into gathering data for this paper. The predation sequences are taken from over 10,000 recorded instances of feeding in these snakes.

Geographic Variation in Bushmasters

In the past, all geographic variations in bushmasters were viewed in a polytypic context, and morphological differences were the diagnostic features by which each “subspecies” was described. Since the bushmasters in this article are treated as “species,” I am for the first time recording morphological variation within the binominals themselves. (The single precedent for this was in Ripa [1994], where Mato Grosso *L. muta muta* and *L. muta rhombeata* were shown to be essentially similar).

The wider its distribution, the more a species can be expected to vary. Hence, *L. muta* with its vast distribution in equatorial South America varies considerably, while *L. melanocephala* with its tiny, almost insular range in Costa Rica exhibits no appreciable geographic variation.

From the available specimens, the South American *L. muta muta* appears to embody at least two distinct forms, a Guiana Shield form and a Western Amazon form.

The range of the Guiana Shield form comprises Guyana,

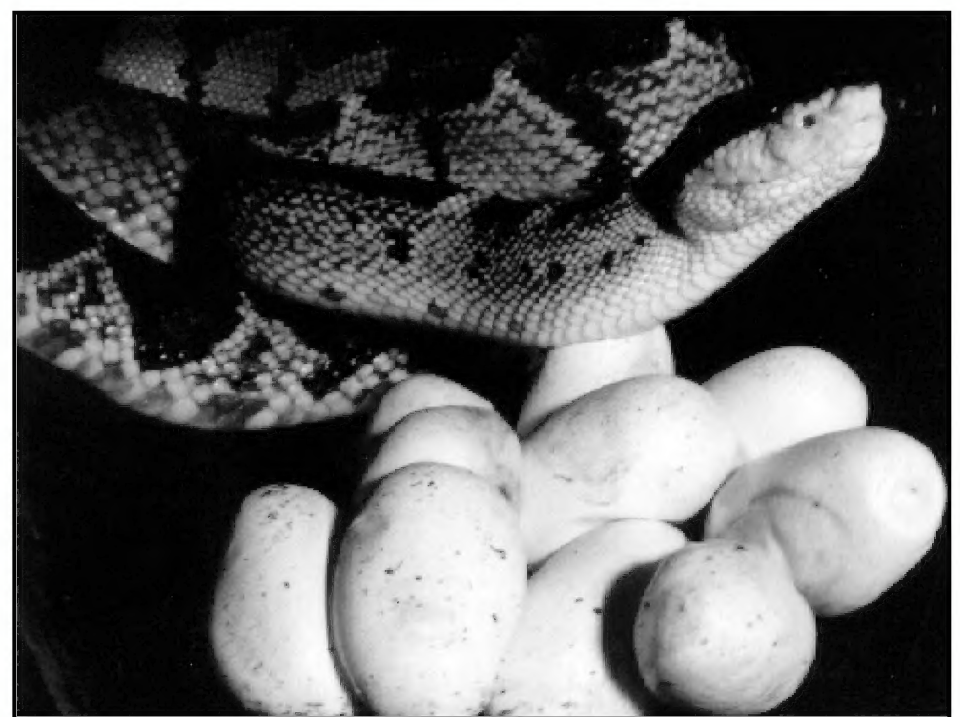


Figure 12. *L. melanocephala* after being prodded off her eggs in the simulated subterranean burrow nest. The female deposits her eggs in the most remote areas of the burrow, guarding them faithfully until hatching 60–77 days later. *L. melanocephala* has the smallest scales of any bushmaster, to half the size of comparable *L. muta* and *L. stenophrys*. The scale is usually surrounded by visible interstitial skin that may be varicolored like the scales themselves. A consistently unelevated frontal region (with respect to the dorsal height of the snout) also distinguishes this species from *L. stenophrys* and *L. muta*.

Surinam, French Guiana, Trinidad, eastern (and possibly southern) Venezuela, and proximate areas of northern Brazil. Here the bushmaster has a smaller, anteriorly narrower head, a more beaded body scalation (with the tubular keel centered along the midline of the scale), larger internasals and canthals, and larger prenasals. The body is more slender. The head markings are much less advanced and usually take the form of a series of small, numerous (up to 40) irregular speckles. The dorsal blotches are not always black; they may be umber, sienna or other dark brown hues.

In the Western Amazon form, there is a north–south affinity in the western Amazon Valley following the Andean versants from northeastern Colombia south through eastern Ecuador and Peru, into northeastern Bolivia, thence east into Mato Grosso State, Brazil. A larger head, a flatter (not very beaded) dorsolateral body scalation with the tubular keel off-center toward the apex, blacker dorsal markings and large distinctive dark head markings, among other traits, distinguish these snakes from those of the Guiana Shield. In some regions, such as along the Rio Pucayacu in Pastaza, Ecuador, the dorsal head markings may be so elaborate as to render the entire head dorsum almost completely black. A wider eastern distribution in the extensive Amazon Basin area is at present uncertain. Whether or to what extent the Western Amazon type is homogeneous with the Amazon Basin snakes (in which case “Amazon Basin form” should undoubtedly supplant it as a more apt name), or if the basin snakes represent some intermediate or gradating form with the Guiana Shield type, or even a distinct form among themselves, a lack of specimens has not allowed me to determine.

The Brazilian Atlantic Forest bushmaster, *L. m. rhombeata* (Hoge, 1965) greatly resembles the Western Amazon form, but is isolated from it. Like the latter, the head dorsum is marked with a distinctive “arabesque” pattern. Like the Guiana Shield form, however, it has enlarged internasals. This form appears to have exceptionally keeled scales, giving large adult specimens an overall “prickly” appearance. Variably, it may have a brighter, more contrasting dorsal body color than the Mato Grosso snake, tending toward yellow rather than reddish-tan. To most observers, however, these two snakes will appear indistinguishable. It seems likely that *L. m. rhombeata* and the southern (i.e., Mato Grosso) populations of *L. m. muta* once formed a continuous distribution. Zamudio and Greene (1997) place the divergence of the Atlantic Forest snakes from Amazonian *L. m. muta* as occurring not more than 300,000 to 800,000 years ago.

The Central American bushmaster (*L. stenophrys*) has two forms, a Western (of Caribbean Costa Rica and Panama west of the Canal) and a Middle Panamanian (vicinity of the Panama Canal Zone east to approximately 79°W)

The Western form is distinguished from the Middle Panamanian form by small internasals, small canthals, a usually blunter, less elongated head, and a generally paler body color. In the Middle Panamanian form the dorsal blotches may be bordered by a whitish-tan through out (unlike the Western form, where this light border usually occurs only posteriorly). Examples from the Pacific extremity of the eastern Canal Zone

range (Cerro Azul region) may have a lower than usual ventral scale count (190 ventral scales in a Cerro Azul specimen, the lowest of any bushmaster seen).

Geographic variation in the South American bushmaster (*L. muta muta*) might reflect paleoenvironmental and climatic changes as recent as the Pleistocene (sensu Potts and Behrensmeyer, 1992; Van der Hammen and Absy, 1994) or paleogeographic events going back much further in time (Zamudio and Greene [1997] refute a “forest refugia” hypothesis as the cause of speciation in *Lachesis*, with a temporal estimate of divergence having a deepest branching in the Tertiary). Certainly the shared traits of the two Central American forms all seem derived from a Western Amazon morphotype, rather than from the geographically more distant Guiana Shield forms. Interpreting the two Central American species to be evolutionarily “newer” than the Amazonian (diverging 11–6 Mya; Zamudio and Greene, 1997), the Western Amazon form can be viewed as the more recently evolved of the two phases of *L. muta muta*. This implies an initial radiation from an eastern rather than a western origin.

The Guiana Shield, a “stable positive unit since the Middle Precambrian” (Stuart, 1966) is the oldest large stable landmass in northern South America that currently has bushmasters. While the age of a landmass does not ensure the origination of a species within that landmass, the unstable orogeny of the frequently deluged Amazon Valley within its early history does not offer as many good opportunities for the development of a highly specialized fauna (having habitat requirements like the bushmaster) as that of the ecologically more reliable Guiana Shield region. Northwestern South America was intermittently flooded until the mid-Miocene, while the eastern Andean area was underwater at various times until the Paleocene (Nygren, 1950; Harrington, 1962; Jacobs et al., 1963). The receding North Andean geosyncline would probably have left the western Amazon Valley a vagarious habitat of partially submerged swampland for an indeterminate period during the Tertiary (pers. interpretation of the literature); and as further subsidence of the Amazon Valley drowned the drainages of the Magdalena, the Cauca, and the Orinoco during the Tertiary (Van der Hammen, 1961; Hoorne, 1994), it is reasonable to suppose that unsuitable habitat conditions for bushmasters might have prevailed there for a considerable period. Thus, while bushmasters are now endemic to the Amazon Valley, it is not unlikely that inhospitable conditions persisting there long after the emergence of the first land bridges might have presented barriers to bushmaster ancestors and early viperids within that region. During a long westward immigration through these developing lowlands, the ancestral Western Amazon forms may have differentiated (from the Guiana Shield forms) even before the next Andean uplift would further segregate this population into East Andean (Western Amazon) and West Andean (Choco) forms.

Similar events seem to have taken place in Central America, although more recently. From the available geological data, the Talamancan orogeny appears to have occurred from northwest to southeast, culminating in the closure of the isthmian link about 3.5 Mya (Savage, 1982; Coates and Obando, 1996).

L. stenophrys appears to have followed a Talamancan route of dispersion such as is seen in other fauna assemblages (sensu Savage, 1966), colonizing these new middle Panamanian lowlands as the portal closed (Figure 13). It follows that the mid-Panama phase of *L. stenophrys* is the more recent arrival from an invasion initiated within the northwestern Talamancan regions of Panama and Costa Rica. *Lachesis stenophrys* stopped short of colonizing eastern Panama due to barriers of unsuitable habitat and/or a pre-existing marine barrier (see below).

Historical notes on speciation in bushmasters, and the controversy of geographic affinity of the bushmaster of eastern Panama–northwestern Colombia and Ecuador

Modern debates over the explanation for current geographic distributions of reptiles in the Americas can be summarized as “vicariance versus dispersal” (Williams, 1989; Crother and Guyer, 1996). In a vicariance hypothesis, barriers of unsuitable habitat arise to isolate faunal lineages so that they evolve independently. In dispersal (I refer here to the “over-water” type), species migrate to new landmasses by way of rafts of flotsam or jetsam and become marooned. The first, vicariance, is somehow “traceable” through tectonic events; while the second, over-water dispersal, is a chance circumstance that can never be proven. Over-water dispersal remains the biogeographic “catchall” for any faunal migration that cannot be explained in terms of vicariance.

Zamudio and Greene (1997), in elevating three of the four subspecies of bushmaster to species, make a case for a vicariant geography shaping two bushmasters, the South American and the Central American, into distinct species. According to Zamudio and Greene (1997) a vicariant geography (the rise of the Andean mountain chain to above 1000 m and the development of high montane vegetation during 18–6 Mya) prevented the intergradation of the two main bushmaster lineages, the cis-Andean *Lachesis muta*, and the trans-Andean *Lachesis stenophrys*, launching the latter upon a distinct evolutionary trajectory (a second vicariant event occurred in Central America, creating a third species). In this section I review Zamudio and Greene (1997) and other related works, and cite evidence generated by a new work, Ripa (in prep.), that shows the Andean uplift was indeed responsible for the evolutionary fate of one population of bushmaster—however, not the population described by Zamudio and Greene (1997).

As mentioned in the introduction, the status of the bushmaster of eastern Panama and northwestern South America is controversial (Hoge and Romano-Hoge, 1981: “till now there is a large gap in the [distribution of] this subspecies and *L. muta muta*”; Campbell and Lamar, 1989: “never determined satisfactorily”; Ripa, 1994: “unresolved”; Zamudio and Greene, 1997: “problematic”). Depending on the source, it can be considered *L. muta muta* (e.g., Hoge and Romano-Hoge [1981] who describe it as inhabiting the Pacific coast of Colombia and Ecuador), or *L. stenophrys* (e.g., Campbell and Lamar [1989] who show a continuous distribution between the two species, and suspect it to be essentially Central American in type). While no scientific evidence supports subsuming this population within *L. stenophrys*, there is a precedent for the

assignment to *L. muta muta*. On the basis of a single example, Martínez and Bolaños (1982) show a range extension for that species in eastern Panama.

In Ripa (1994) I questioned this inconsistency. Intergradation among the bushmaster species (then subspecies) had never been confirmed, and there was no factual basis for a belief in sympatry or intergradation. Remarking Campbell and Lamar’s (1989) “geographic affinity” idea, yet unable to dismiss Martínez and Bolaños’s (1982) find of an apparent *L. muta*

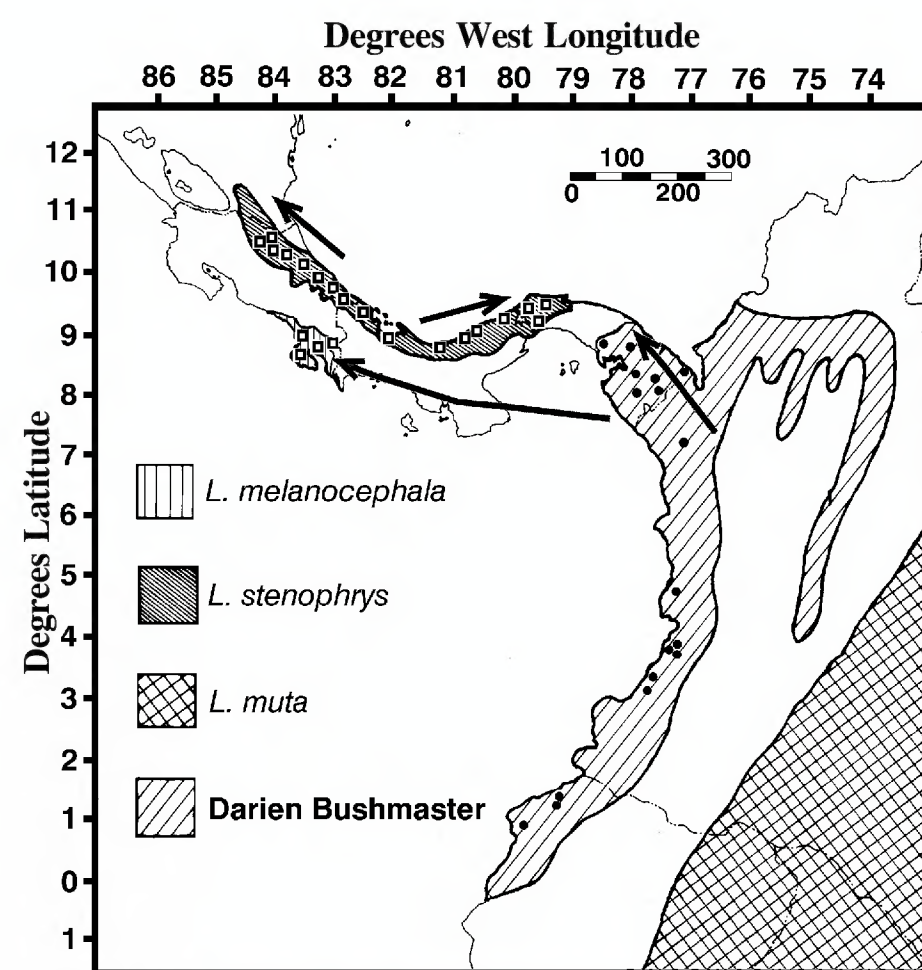


Figure 13. Geographic distributions of the bushmasters of Nicaragua, Costa Rica and eastern Panama–northwestern South America (modified from Campbell and Lamar, 1989). Distributions of *Lachesis stenophrys* and *L. melanocephala* are shown west of longitude 79°00'W. Distribution of the western Andean form, called “Darien bushmaster,” is shown east of 78°50'W, and extending south to just below the equator. Despite proximity, these snakes maintain their own morphological identities on either side of the Tropical Dry Forest barrier that separates them, indicating low gene flow between ancestors. A possible zone of intergradation between the two populations, in the narrow San Blas corridor, has not been proven and is not depicted.

Arrows indicate probable dispersal routes based on morphology. *L. stenophrys* followed a Talamancan fauna dispersal route (sensu Savage, 1966), advancing along a northwestern route into Nicaragua, where it was held back by the Nicaraguan depression. Advancing southeastward across the lowlands of Caribbean Costa Rica and northeastward into an emerging middle Panama, it was held back by another marine barrier from penetrating eastern Panama. During this period, the ancestral Darien bushmaster was probably already endemic to eastern Panama on an enduring landmass called the “Panama spur” (sensu Lloyd, 1963), perhaps the original source of the westward invasion into Pacific coastal Costa Rica (or western Panama during a climatically different glacial period). When the Panamanian portal closed in the late Miocene or early Pliocene, areas of unsuitable habitat (Tropical Dry Forest) persisted to bar further eastern colonization by *L. stenophrys*, and western colonization by the northwestern South American form. Today these two allopatric and morphologically distinctive snakes exist within 100–150 km of each other, separated only by this vegetation barrier. The occurrence of the “Darien bushmaster” in the inter-Andean valleys of Colombia is inferred on the basis of Campbell and Lamar’s (1989) report of bushmasters occurring in these regions, and from the lack of barriers to prevent it.

muta in eastern Panama, I questioned the identification of the specimen, but could not invalidate it. Zamudio and Greene (1997) thought that interbreeding in nature between Central and South American bushmasters was “highly unlikely,” due to the Andean barrier, and followed the “geographic affinity” idea of Campbell and Lamar (1989), stating that “the Choco populations of *Lachesis* are probably referable to the widespread Central American taxon.” (It is worth noting, however, that the “Choco population” is really the widespread one, with a total distribution range in eastern Panama, northwestern Colombia and Ecuador exceeding by some 4–5 times the combined size of the range of both Central American bushmasters.) But at no point had a systematic analysis been made comparing this population to the other bushmaster species. Even Martínez and Bolaños (1982) limited themselves to describing a single specimen (having no other), and called it *L. muta muta*. What is telling here is that Martínez and Bolaños (1982) were describing a “range extension” only and making no case for or against the existence of *L. stenophrys* in eastern Panama. Which suggests that to many authorities prior to 1982 it was normal to think of the bushmasters of northwestern South America as *Lachesis muta muta*.

When Zamudio and Greene (1997), using mtDNA sequencing, a “molecular clock,” and the available paleogeographic data on northwestern South America, confirmed my 1994 view of distinct South American and Central American clades, they made their case on evidence for the Andean chain having separated the two main bushmaster lineages. However, there was a logical condition: if the evolutionary divergence of “trans-Andean” *L. stenophrys* from cis-Andean *L. muta* was to be shown relating to the Andean uplift, the western Andean population had to be *L. stenophrys*.

And yet there was no evidence that it was. On the contrary, the only published evidence (i.e., the specimen of Martínez and Bolaños [1982]) was that these snakes were *L. muta muta*. Of course, there was the alternative: Martínez and Bolaños (1982) were “wrong.” Which is to say the diagnostics of *L. stenophrys* in other literature (Peters and Orejas-Miranda, 1970; Solórzano and Cerdas, 1986) were wrong also. In other words, the diagnosis of *L. stenophrys* as it stood would need to be enlarged in order to accommodate the Martínez and Bolaños (1982) specimen.

I do not find this to be the case. As these tables show, *L. stenophrys* is morphologically distinctive within a given distribution range (see Figure 13), and in accord with the accepted diagnosis of that species, is not conspecific with the bushmasters of eastern Panama–northwestern Colombia and Ecuador.

No less distinctive is the “Darien bushmaster” itself. Closest in appearance to the lineages of the Western Amazon (see preceding section), its nearest resemblance to a Central American species is not to *L. stenophrys* at all, but to *L. melano-*

cephala (which has a distribution restricted to a comparatively tiny corner of southeastern Costa Rica). This contradicts the “geographic affinity” idea of Campbell and Lamar (1989) and Zamudio and Greene (1997), and supports the earlier view of Hoge and Romano-Hoge (1981) and Martínez and Bolaños (1982). These snakes are of distinctly South American affinity.*

Figure 13 shows the present-day distribution of *L. stenophrys* in Central America. The easternmost extremity of its range in Panama abuts a Tropical Dry Forest belt that dominates the topography of the narrow isthmian pass south of the San Blas mountain range (vicinity Chepo region, Panama province, approx. 79°W, 9°N) (Holdridge, 1964; Ministerio de Obras Publicas Panama, 1993). Tropical Dry Forest is unsuitable habitat for bushmasters (Vial and Jiménez-Porras, 1967; Campbell and Lamar, 1989; pers. obs.). Further buffering this zone on the east is a yet larger expanse of Tropical Moist–Dry Transition Forest, which envelopes the eastern periphery of the Tropical Dry Forest. This latter zone, while not uninhabited by bushmasters (but only of the northwestern South American type), supports only a very sparse endemic population, becoming even more sparse toward the west (pers. obs. and testimony of local residents, evidence supported by small number of museum samples and lack of accounts in the literature). Thus, two vegetation barriers contribute to preventing contact between the lineages of Costa Rica–western Panama (*L. stenophrys*) and those of eastern Panama–northwestern South America (Ripa, in prep.).

At first glance this region appears to be of somewhat questionable significance as a barrier. Extending 100–150 km along the length of the northern (Caribbean) coast of the narrow isthmus, it offers a slender corridor of apparently suitable Tropical Moist Forest habitat. This corridor, literally the San Blas mountain chain, would appear to unite the habitat of the eastern Panamanian bushmasters with that of *L. stenophrys*, acting as a conduit between them. With this “hole in the dike,” one wonders that the Tropical Dry Forest belt beneath the San Blas chain can truly be considered a “barrier” at all—and indeed, if the bushmaster were a more adaptable kind of snake it probably would not be (e.g., it is not a barrier to *Bothrops asper*). Prior literature has assumed a continuous distribution between the two forms. And yet both forms maintain their morphological identities at either range extremity, on both sides of the dry forest. If interbreeding or coexistence occurs within this part of the San Blas chain (never shown as of this date), it has not had a significant effect upon either population. The effectiveness of this barrier is historically verifiable by the forms of the snakes themselves.

The success of this barrier can be construed as resulting from: (1) The low density of bushmaster populations in general; the limited available habitat (within the upper versants of the narrow San Blas chain) cannot support large numbers of either population. (2) The marine barriers that lie on either

* Describing the Darien bushmaster as a species distinct from *L. muta*, contradictory as it is to the vicariance hypothesis for *L. stenophrys* and *L. muta* in Zamudio and Greene (1997), does, however, confirm their idea in a new and unexpected way. The Andean uplift was a significant barrier to colonization by Amazonian *L. muta* in that it permitted the development of a distinct trans-Andean trend in the bushmasters of northwestern South America (but not in *L. stenophrys*), although one less morphologically distinct from that clade than either of the two Central American forms themselves. This “Darien” or “Choco” bushmaster, with its stocky body, strong lateral body compression, and more developed middorsal ridge (among other characteristics), appears moving toward a specifically Central American design, albeit retaining many more characteristics of the cis-Andean *L. muta*.

side of it, the Caribbean Sea and the Pacific Ocean, have prevented the main lineages from bypassing the dry forest barrier. (3) The underlying terrain is geologically young, and replaced a pre-existing marine barrier.

In support of point 1, we have Island Biogeographic Theory (Marshall et al., 1982), which demands that the effect of a source fauna on another fauna receiving immigrants should be proportional to the size (or diversity) of the source fauna. Here the number of immigrants into the range extremity of either species would be small, and their effects negligible upon the receiving fauna.

In support of point 2 we have the proven effectiveness of marine barriers with regard to this species. In an over-water dispersal hypothesis, fauna swept off on rafts of flotsam or other debris are marooned on islands of favorable habitat, which, over the course of time become part of larger more “permanent” distributions. But there is no evidence that this type of dispersal works for bushmasters. Zamudio and Greene (1997) make a significant observation: the absence of bushmasters in Panama’s Bocas del Toro archipelago. While the lack of bushmasters in Bocas del Toro may be due more to poor habitat than to an inability to cross the small sea barrier (contradicting the reason given in Zamudio and Greene [1997], but not the factuality of the occurrence; but see below), it is true that open sea appears to inhibit colonization by these snakes. We do not find bushmasters in Atlantic coastal Nicaragua, in spite of suitable habitat ranging for hundreds of kilometers. Indeed, bushmasters do not occur anywhere north of the Nicaraguan Depression, a former marine portal which appears to have limited bushmaster distribution prior to its Pliocene closure. We do not find bushmasters in Honduras, Guatemala, Belize, or anywhere in nuclear Central America—they are strictly an isthmian phenomenon (a very good argument against bushmasters having colonized South America from the north). We do not find bushmasters on any islands, even close-lying ones, which are numerous off the Atlantic coasts of Panama and Colombia (and which are inhabited by other pitvipers, such as *Bothrops*). Even the population of *L. muta* on Trinidad is explainable by prior contact of that continental shelf island with the mainland (Zamudio and Greene, 1997, sensu Henderson and Hedges, 1995). Barbour (1914), arguing against over-water dispersal occurring in reptiles, points out, “If this [over-water dispersal] has taken place in the past, it should be occurring still, and the fact that it does not now occur is good proof that this method of dispersal has never played a part of any importance in the past.” Certainly, if chance circumstances ever did disperse bushmasters over-water these same circumstances do not appear to be happening today. Bushmasters have enough trouble adapting to secondary forest and agriculture, much less enduring long sea voyages on flotsam to colonize novel ecologies. Of all barriers to invasion, the marine barrier appears to be the most effective.

The special habitat needs of bushmasters have undoubtedly contributed to the poor success rate of marine invasions, perhaps as much as the ocean barriers themselves. Bushmasters do not adapt well to hot, dry seacoasts, and, equally, avoid lowlands and swamps. They favor elevated inland terrain,

relatively cool and humid; they have a low heat–dryness threshold, and exposure to solar heat apparently kills them out of deforested areas in which other normally coexistent pitvipers, such as *Bothrops asper*, thrive (hence their absence from Bocas del Toro is the result of unsuitable habitat). The special hydration needs of the eggs, which are exposed to ambient conditions in an underground burrow shared by the mother snake, and not abandoned in moist humus, make dry habitat unsuitable (Ripa, 1994). Similarly, the bushmaster’s skin, adapted to very humid (but not constantly wet) microhabitats, is prone to dysecdysis during the skin shedding cycle (Burchfield, 1975; Boyer et al., 1989), requiring a high moisture contact during the last five days before the skin is shed (Ripa, unpub. data). Conversely, an overly moist environment causes an often fatal skin condition (Ripa, unpub. data). Low, frequently flooded terrain, such as also prevails on many islands and coastlines (and occurs also in Bocas del Toro), is equally unsuitable for egg-laying in an underground burrow situation. Note that bushmasters are not found along the low coastlines of Surinam and the Guianas; and they avoid the frequently flooded Barra del Colorado region in Costa Rica. Even in the Atlantic Forest of Brazil they avoid coastal jungle and are typically encountered only at high elevations (pers. obs. in Brazil). Thus the actual “body of water” is not the only barrier to colonization by these snakes, but the nature of the coastal environment itself, which is usually either swampy or very dry.

The narrow corridor of apparently (but not provenly) suitable habitat within the San Blas chain is of just such a questionable nature. On the low coastal (windward) versants to the north the habitat is hot and dry. On the leeward versants to the south occurs intermittent “rain-shadow” conditions, such as are often associated with xeric vegetation. Further south is the Tropical Dry Forest belt itself, buffered on the east by Tropical Moist–Dry Transition Forest. The former is completely unsuitable to bushmasters; the second is of limited utility, bushmasters being only rarely found there. This part of the San Blas chain, although classified as Tropical Moist Forest, is really not such good bushmaster habitat as it might appear.

Point 3 maintains that the success of the dry forest barrier results not only from its present-day potential, but from its geologic history. The region that currently separates these snakes is itself the relict of a former marine portal, one of the last land masses during the Cenozoic to connect Central America with South America (Stuart, 1966; Coates and Obando, 1996). In older times (less recently than 3.5 Mya), it was open sea.

The developing isthmus failed to reunite the two bushmaster lineages in northeastern Panama because it (1) provided unsuitable habitat; and (2) *L. stenophrys* is in itself a recent immigrant into middle Panama owing to a prior sea barrier dominating the region since before the Pliocene. *L. stenophrys* would have had to colonize the coalescing middle Panamanian isthmus by a Talamancan route of dispersal (sensu Savage, 1966); that is, from northwest to southeast. Its present-day near juncture with the Darien snake occurred not more recently than 3.5 Mya.

Undoubtedly, the ancestral Central American species (*L. stenophrys* and *L. melanocephala*) split during the uplift of the Talamanca mountain chain (just as Zamudio and Greene [1997]

say they did). This event occurred in the late Miocene or early Pliocene (8–5 Mya) and predated the Pliocene closure of the Panamanian Portal. Thus, the two Central American species were probably already on their own separate evolutionary trajectories prior to the most recent geological reconnection of Central America with South America (occurring 3.5 Mya; Coates and Obando, 1996).

Zamudio and Greene (1997) do not account for this historical disparity. Perceiving the northwestern South American form as Central American in type, they offer no explanation as to how their ancestral “*L. stenophrys*” with its apparently “continuous” distribution in Central America made it across the unformed isthmian link (a sizeable ocean barrier whose geologic age far surpasses that of the Andean mountain barrier) in time to diverge at 8–5 Mya. Yet they are aware of a problem. They state, “Finally, our conclusions that the initial divergence within bushmasters [in the Andes] predates the Pliocene closing of the Panamanian portal underscores a continuing enigma in Middle American biogeography, the interchange of terrestrial organisms across what is usually portrayed as a marine barrier.” An ancient marine barrier existing between their ancestral northwestern South American “*L. stenophrys*” and their ancestral Central American “*L. stenophrys*” leaves quite a hole in the evolutionary story. It becomes still more enigmatic when one postulates vicariance affecting some populations (such as the Andean and the Talamancan) but not another, such as their “*L. stenophrys*,” which prior to 3.5 Mya would have occupied two separate populations, each quite effectively isolated. At some point vicariance evolution runs out of steam, and has to fall back on over-water dispersal in order to transport its ancestral material over a pre-existing ocean barrier to the Talamanca mountain range in time for an 8–5 Mya uplift (where the species will diverge yet again), for there will be no land bridge to take them there until 3.5 Mya. Their ancestral “*L. stenophrys*” (we must infer) simply jumps the ocean gap from northwestern South America into Central America at some point after the Andean uplift, establishes itself as a second population, and then is reunited as a single population at 3.5 Mya when the Panamanian portal closes.

Obviously this is not what happened. Nor can we look further back into the past and argue convincingly for vicariance geography splitting a continuously distributed single ancestral species into two allopatric forms. Present geographic knowledge does not admit even a possibility of a reconnection between Central and South America (and thus a continuous distribution between these snakes) existing more recently than 90–60 Mya (Lloyd, 1963; Stuart, 1966; Pindell and Barrett, 1990; Gentry, 1982; Crother and Guyer, 1996). This last event would, according to modern interpretations of crotaline age, predate the arrival of pitvipers into the New World (Cadle, 1987; Kraus et al., 1996). But even if we extend the deadline of “30 million years” (of existing crotalines) to fit our requirements of a needed land connection in isthmian Central America (or do the opposite and place the Talamancan divergence (8.5 Mya) occurring more recently than 3.5 Mya), we are still caught in a disparity: the Darien bushmaster is morphologically closer to *L. melanocephala* than to *L. stenophrys*. Thus it is unlikely if the ancestral Darien snake was the immediate

ancestor of *L. stenophrys* in the first place. The bushmaster invasion into isthmian Central America probably began not on the north (Caribbean) side of the Talamancas (occupied by *L. stenophrys* today), and which is most remote from northwestern South America, but on the southeastern side, currently occupied by *L. melanocephala* (and closest to northwestern South America). In other words, the northwestern invasion of *Lachesis* into Central America was probably initiated within the Pacific region, not in the Caribbean. The ancestral Darien snake was the immediate ancestor of *L. melanocephala*, and *L. stenophrys* emerged from this complex. In short, a continuous inter-American distribution between ancestral Central American *L. stenophrys* and ancestral northwestern South American bushmasters probably never occurred.

But where was the ancestral Darien form prior to its northwestern radiation? Long before the Talamancan uplift split the ancestral Central American complex (*L. stenophrys* and *L. melanocephala*) into their separate evolutionary trajectories, and even before the developing Choco lowlands emerged as a series of land bridges to the Central Andes, the ancestral northwestern South American bushmaster may already have been established in eastern Panama.

From Stuart (1966): “In the Pacific coast, west of the present shoreline of Colombia and Ecuador, there existed a land mass which extended into eastern Darien, this last the ‘Panama Spur’ of Lloyd (1963). According to Harrington (1962) this western borderland may have persisted from the Paleozoic until the Pliocene (mid-Miocene, according to Nygren, 1950). Between this western borderland and the emerging Andes, the Bolivar Geosyncline was initiated during the Eocene. This channel, extending from the Caribbean to the Gulf of Guayaquil, was completely flooded, with the exception of occasional emergent bridges between the Cordillera Central and the western foreland, from the lower Oligocene until middle Miocene, when sediments from the now-high western Andes began filling it (Nygren, 1950).”

Older than the Choco lowlands (which were largely under-

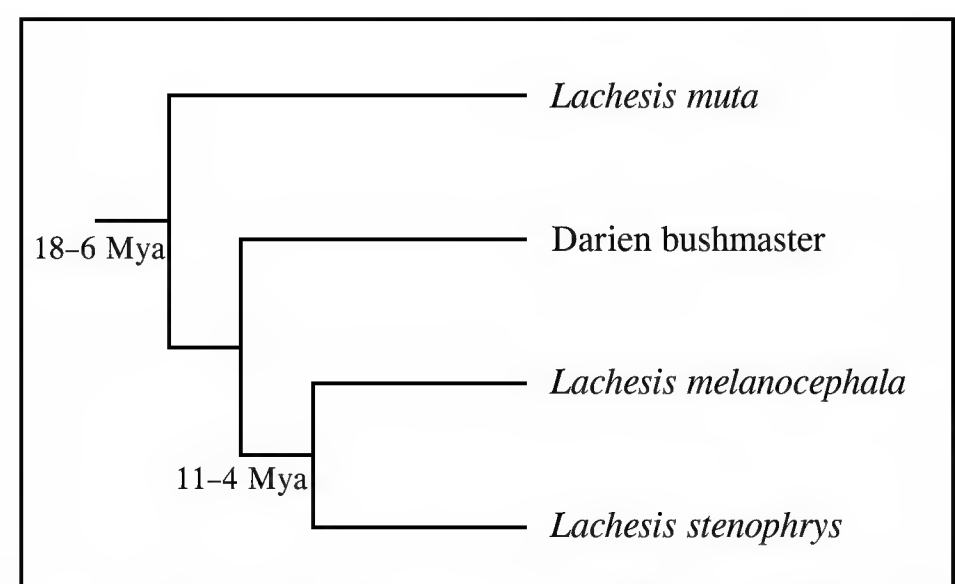


Figure 14. Summary diagram of the evolutionary history of *Lachesis* populations, based on a vicariance–dispersal explanation. Modified from Zamudio and Greene (1997). The lineage that gave rise to the Darien bushmaster also gave rise to the ancestor of *L. melanocephala* and *L. stenophrys*. The time of evolutionary divergence of this ancestral Central American clade from the Darien bushmaster is unknown, but is presumed to have occurred prior to the divergence of the two Central American clades.

water until the mid-Miocene), older even than the Andes themselves, is the enduring “Panama Spur.” The present-day range extremity of the Darien snake in eastern Panama describes almost perfectly the arc-like outlines of this then isolated land mass. Did an “island-bound” population of ancestral Darien bushmasters distribute its genetic material from the Panama Spur into the northwestern regions of the evolving Talamanca ridge contemporaneous with the mid-Miocene rise of the Andes? It seems reasonable to suppose that the oldest region providing the nearest contact is likely the region that provided the contact. To the south we have only the younger Choco lowlands, and the unstable Andes themselves. If the Panama Spur did indeed harbor the ancestral “missing link” between these snakes, then we should expect to find a genetic affinity (a telltale sign of that prior lineage) to one or both Central American species within the populations of the Darien. But that affinity need not be repeated in the southern lowlands of the Choco and northwestern Ecuador, whose source fauna may have arrived by a different route (such as through mountain passes from the eastern Andes during glacial climate changes; sensu Potts and Behrensmeyer, 1992). The ancestors of the southernmost assemblages of northwestern South America need not have participated in a northwestern radiation at all.

The geologic stability of eastern Panama (within the Panama Spur), and the presence of bushmasters in this region in the modern day, suggests that bushmasters occupied this region long before the Pliocene closure of the Panamanian portal. The proximity of the Panama Spur to the southern versants of the emerging Talamanca range would make it the obvious transit point for a northwestern radiation. But in the absence of a known land bridge to carry our immigrating population into isthmian Central America, we still cannot answer how or when that event occurred.

Prey size and predation frequency

The “large predator = large prey” hypothesis seems the most convenient explanation for the bushmaster’s great size. One expects nothing less from the world’s biggest pitviper than that it will be able to consume prey comparable to other large viperids, especially *Crotalus*. None of this, however, is grounded in fact. If anything, my data reveal just the opposite. The adult bushmaster is uniquely the most inefficient swallower of any large viperid snake in the world.

Like many behavioral discoveries, this disparity in prey size was noticed by accident: one day I realized that an inordinate number of prey items were being wasted by the snakes. Rodents (*Rattus norvegicus*) exceeding certain dimensions were being killed and left uneaten. Similarly, thawed, frozen rodents (warmed to simulate live prey) were being strike-held, but not swallowed if they were over a certain size. Strangely, the carcasses had been partially swallowed, with the fur lathered (with the snake’s saliva) up to the prey’s shoulder region, or just beyond. The snakes had tried to swallow the prey, and yet for some reason had given up the attempt, even though the prey was well within a size range one could expect other large crotalids to be able to take. Prey items that even smaller rattlesnakes, for example, would have no difficulty in swallowing,

were for some reason not being eaten by the bushmasters.

As this phenomenon occurred equally among some 40 large wild-caught bushmasters, whether live or dead prey were offered, and with regularity from year to year, it soon became apparent that the phenomenon must be motivated by something other than aborted feeding reactions in “not very hungry” snakes. Eventually, a feeding regime evolved to leave off offering any prey that exceeded a specific size threshold, because it was evident that it would not be eaten (several hundred rodents having gone to waste by now over the course of time). I arrived at the average prey threshold given in Table 4 as a “safe bet” for presenting ingestible prey in order to avoid wastage of the food item. To attempt to quantify this further, I then recorded 100 sequences (of each species) observing swallowing capability vs. regurgitation of partially swallowed rodents exceeding 300 g (for *L. muta*) and 350 g (for *L. stenophrys/L. melanocephala*). Average girth of swallowable prey was not greater than 20 cm. The swallowing attempts were observed from start to finish. When the rodent exceeded the maximum size threshold, it was disgorged before swallowing was completed. In many cases, the snake’s quadrate region had not surpassed the shoulders of the food animal when the prey was disgorged; in other instances the prey was disgorged when the angle of the jaws had reached or surpassed the prey’s midbody; in yet other instances the regurgitation process began when the prey was nearly down the snake’s throat, but impeded by the haunches and the hind limbs at the angle of the snake’s jaws. No bushmaster regardless of size (some specimens here reach 10 kg) would swallow any rodent exceeding 25 cm girth and a weight of 595 g. Moreover, these huge prey items (for a bushmaster) invariably proved too large to be digested by the snakes, and were regurgitated undigested within five days. Apparently, so large a meal turns to poisonous carrion before it can be assimilated, and must be expelled. By contrast, the largest prey item ever swallowed *and digested* did not exceed 525 g. Multiple prey items, on the other hand, could in total weight reach and in some cases even surpass the single-prey-item size threshold without being regurgitated by the snake. Bushmasters scored a low to very low relative swallowing threshold compared to *Bothrops*, *Bothriechis*, *Crotalus*, *Bitis* sp., and all boids. My estimation is that pound for pound the adult bushmaster has the lowest relative swallowing threshold of any viperid snake, with a maximum prey-size capacity in an adult snake of 5000 g (3–6 yrs of age) not exceeding 12% of snake body weight, but more typically not more than 6%. Double this snake size and the prey size percentage rate will be halved, till the maximum prey size will not exceed 6%. Neonates and sub-one-year-old examples with their proportionately larger heads and more flexible/distendable throats can, by contrast, consume as much as 30–40% snake body weight (although rarely the latter figure). This ratio changes little for the first 6–8 mo (80–100 cm) of the snake’s life; thereafter dropping markedly, until at last a bushmaster of 250 cm or larger has little greater swallowing advantage over a bushmaster of only 150–170 cm (provided the latter is sexually mature).

Boyer et al. (1995) remark adult bushmasters being able to swallow prey of 40–50% snake body weight in a single prey item. This is completely unfounded. To translate this 40–50%

swallowing feat into adulthood would be to postulate a 5000 g bushmaster, with a head smaller than the width of a credit card, and a neck smaller than a U.S. 50-cent-piece, capable of engulfing a prey item in excess of 2000 g, or the approximate size of an adult cottontail rabbit—a size three to four times the capability of even the largest bushmaster at 10 kg. The swallowing capacity of bushmasters is in no way similar to those of *Crotalus*, or large *Bothrops*. Greene and Santana's (1983) anecdote of a 90 cm bushmaster consuming a prey item of "40% its mass" is an accurate (if freakishly extreme) example of what a neonate or six- to eight-month-old bushmaster can do (see growth rates). For, although not noted by Greene and Santana (1983) a 90 cm bushmaster is technically still in "baby" category, only a little more than twice its length at hatching, with a weight of not more than 500–700 g. The diameter of its body is smaller than that of a standard household "D" battery; coiled up it can squeeze into a large coffee mug. Such a bushmaster can by no means be considered an "adult." Nor can one draw conclusions about the swallowing thresholds of adult snakes based on the capacities of neonates and juveniles. An infallible rule is that the swallowing threshold of young and neonate serpents is *always proportionately higher than the adult threshold in all snake species*. Proportionately larger heads, stockier bodies, and more flexible throats and body cavities account for this, an evolutionary advantage conferred upon the young to insure that they will always be able to catch an ingestible meal.

Growth relationships of head proportion to body size in crotalid snakes are well established (Klauber, 1972). While there is a size shift toward greater head size in the mature adult snake than in the young adult snake, as occurs in the normal general thickening of the body; this size shift increase in mature snakes is much less than the proportionate head size reduction of the maturing snake as its growth exceeds the neonate and young snake stage. The head and body proportions of an adult bushmaster and a baby bushmaster are very different. As the length of the bushmaster increases with age, its relative

head size (and relative body girth) does not increase as much. As such, a 2.5 m bushmaster will have a head size not much greater than a 1.7 m one (if both are sexually mature). Expressed in visual terms, if the adult bushmaster maintained the same proportions as the neonate, a 2 m bushmaster would have a head bigger than a man's hand (instead of the approximate size of a credit card as it actually is), and with a body girth equal to a man's thigh (instead of its normal girth, usually not greater than a man's forearm). The result of the added length in the larger bushmaster is a capacity to engulf *more prey*, but not prey of a greater size.

Greene (1983) remarks prey diameter in relation to snake head size (ingestion ratio) and prey mass in relation to snake mass (weight ratio) having a strong correlation. This is certainly true, and supportive of the idea of an ontogenetic shift that puts baby and young snakes in the position to eat *relatively* larger prey than the adults they will become.

Yet even a 40% meal size for a 90 cm bushmaster is testing the extremes of what is possible for these snakes (Figures 15–18). Without challenging Greene and Santana's (1983) important observation, it must be agreed that these workers were doing field studies whose aim was not to determine prey size but to observe bushmasters under natural conditions, and to disturb the animals as little as possible. Their remarks are that a bushmaster of "90 cm ate a rodent weighing at least 40% of her mass." The nonspecific term "rodent" suggests the prey animal was not identified except as a visible mass in the snake's stomach. The writers' use of "at least" and "mass" as opposed to giving a precise weight suggests that a *visual* estimation had been made, and that a precise snake weight after feeding was probably not known (since no descriptions of the snake killing and eating the rodent are provided, we must assume this was not seen: the small size of the snake and the large size of the prey forbids the possibility of the prey being strike-held, and a rodent of the proportions given [40% that of approx. 600 g, the weight of a 90 cm bushmaster], would



Figure 15. A 230 g rodent with a 600 g bushmaster (*L. melanocephala*), of 90 cm. This 39–40% snake body weight prey item represents the upper threshold of what the young (sub-1-year-old) bushmaster can swallow (but not digest). However, as the snake grows beyond this size the ratio of prey size to snake size drops radically, till at last a 2.5 m bushmaster has little greater swallowing advantage over a 1.7 m one. Common household batteries serve to indicate the small girth of the 100 cm snake, which is only 6–7 mo old.



Figure 16. A dead neonate *L. stenophrys* (upper) with its 7-month-old, 100 cm, 700 g litter mate (right). When fed large prey, bushmasters grow very fast; however, the rodent in this shot (at 230g, or 32% snake body weight) is at the very top end of what the 700 g snake can successfully swallow *and digest*. This bushmaster already has a 7% snake body weight meal inside it.

probably survive a great number of minutes before dying from the venom [based on typical observations in captivity] which would require the snake to trail it for a considerable distance [as trailing relates to movements, and their study was about movements, we must assume trailing would have been mentioned also if it had been seen]]. To catch and weigh the young snake after feeding would have compromised the intent of the study (that of not disturbing the snake) so this was probably not done. A “40% mass” thus visually ascertained might be attributable to other things than the physical weight of the prey animal. In addition to the displacement bulk presented by the rodent body, it might represent rodent fur (fur of *Proechimys* sp. is considerable, and may drastically increase the apparent “size” of the mammal itself); feathers (bushmasters will eat birds); and inevitably, gas bloating of the prey animal itself which will swell up with gas to double its own girth within the first 12 hrs during snake digestion (causing a 20% meal to look like a 40% one). It might also represent multiple prey items, which could not be ascertained through the body wall of the snake, and with all of the other above contingencies added in as well.

Figures 15–17 show some common household batteries, from which the reader can deduce the snake’s girth and the added displacement of the prey item once engulfed (since I have not been able to induce a captive bushmaster of this size to eat such large prey, we must content ourselves with this less satisfactory comparison). With gas bloating of the 40% prey item, the snake would not only have difficulty crawling, it would be nearly asphyxiated from the outward pressure on the snake’s lungs. The snake’s digestive acids would be unable to keep up with the rapid decay of the prey animal, which would become toxic to the snake, and probably necessitate its disgorging the overlarge meal within a few days (judging from frequency of regurgitation of outsized meals in captivity), if the snake did not die from its huge meal in the interim. This is not to challenge Greene and Santana (1983); I believe their observation of “a 40% prey item” has actual validity as the top end of what would be possible in a 90 cm bushmaster. In other

words, it is within the realm of possibility that a 90 cm, 500–600 g bushmaster (but not a 150 cm, 2500 g bushmaster) *could* have swallowed a 40% snake-body-weight rodent (it is not as probable that it could have digested it). Only in the neonate and very young snake do we note prey of such proportionately large size being consumed. Yet even here the feeding threshold is more limited than what one could expect for a comparably sized *Bothrops*. Note that in 50 feeding attempts with 25, 90 cm bushmasters offered 40% snake-body-weight prey, not one example was able to engulf the rodent (nor were any able to strike-hold it while alive, although the attempt was made; some of the strike-released prey took over 30 minutes to die!). In all cases the oversized prey item was disgorged before the snake’s jaws could surpass the prey’s shoulder and midbody region. A 175 g rodent is the most that I have ever seen swallowed in a snake of this size (but it could not be strike-held). However, while I am willing to grant that in exceptional circumstances a prey item 40% of the snake’s body weight *could* be swallowed, it is highly doubtful if a 90 cm bushmaster could *digest* such a huge meal in any event (in 12 out of 20 cases of 600 g *L. stenophrys* swallowing 175 g rodents — a 30% snake-body-weight meal — regurgitation of the undigested meal resulted in 4–5 days). In Figure 17, note the tremendous girth of the 45% snake-body-weight prey item compared to the snake’s body girth. Realize that this girth will double as the rodent carcass expands with gases in the snake’s stomach. Note that the carcass will be thoroughly rotten before the snake’s digestive acids can even penetrate its skin and fur — a period requiring not less than 3–5 days if the entire prey item could fit within the snake’s stomach (which it can’t, because the posterior portion of the prey animal is projected well into the snake’s anterior oesophagus and must remain there until the digestive processes can allow the head portion to pass on). We do not know, from the Greene and Santana (1983) report, if the 90 cm snake *actually did digest* the prey animal, only that after nine days it “moved to a new site” (perhaps it vomited up the mass somewhere in between).



Figure 17. This 320 g rodent (left), at 45% snake body weight, is outside the capacity of this 700 g bushmaster (far right) to digest, and probably to swallow. Were it to be swallowed, the mass would rot and turn to poisonous carrion in the snake’s stomach faster than the snake’s stomach acids could penetrate the rodent’s skin and fur. The snake must then regurgitate the mass, or perish with the now toxic food item inside it.



Figure 18. Neonate with a 40% snake body weight meal size. Swallowable, and digestible in neonates, but not in adults, where the maximum meal size that can be engulfed drops to 6–12% in a snake of 5000+ g. Note the relatively larger head compared to body girth of neonates, increasing the swallowing opportunities of young snakes. This does not translate into the adult snake; compare with Figure 19.

On the basis of this single example of a sub-one-year-old bushmaster observed to have fed in the wild, the authors conclude: “The hunting strategy of the *L. muta* seems to be, find a ‘good’ place to ambush prey, feed infrequently on large items, and minimize detection by enemies.” An irreducible conclusion on the basis of that single young animal, and one that might be applied to every other viper in the world. Certainly no one, the present writer included, could have expected that adult bushmasters would not follow this predictable pattern as well, especially one observed in so many other crotalids. And yet the feeding thresholds of adult bushmasters, as we have seen, are relatively small for a snake its size, and *require the bushmaster to feed frequently*. Subsequent reporters taking the Greene and Santana (1983) anecdote as a signal flag for adult bushmasters being able to consume massive prey items in the manner of other large crotalids, have been willing to stake entire hypotheses on the swallowing potential of that single little 90 cm snake. We observe an example of this later in Boyer et al. (1995), where an attempt to translate the swallowing potential of the very young and neonate bushmaster (based on Greene’s and Santana’s 90 cm “baby”) into that of the adult results in a behavioral impossibility. (See following sections).

Discussion: A uniquely inefficient swallower

The presently held notion of the adult bushmaster being able to engulf massive prey in the manner of other crotalid snakes (40–50% of their body weight: Boyer et al., 1995; Greene, 1986) is without factual basis, and casts a false light on the natural history of these snakes. The truth is much more interesting in that it sheds an unexpected light on the great physical size of these snakes (in a more intriguing way than the old “large predator = large prey” hypothesis) and on the relationship of snake size to habitat and vertical distribution. More immediately, it may explain the type of prey bushmasters eat—and do not eat. We will begin with the latter.

The oft-printed remark in popular literature that bushmasters feed on prey animals as large as adult agoutis (*Dasyprocta* sp.) is without factual basis. Agoutis, averaging 1.3–4.0 kg (Nowak, 1991), are well outside the capacity of any but the bushmaster to swallow. Even the smaller acouchis (*Myoprocta* sp.), which average 600–1300 g, are probably outside the threshold of any but the very largest bushmasters to swallow. And no bushmaster could ever swallow a paca (*Agouti paca*), which even at birth exceed 700 g. In the bushmaster, then, we have a very large viperid snake reaching a body size comparable to some of the medium sized pythons, and yet with a swallowing capacity much below what one would expect for a snake its size.

Growth size of snakes relates to size and amount of prey intake. And growth shape of snakes relates to shape of commonly eaten prey, in many cases. Hence, the snake-eating king cobra (*Ophiophagus hannah*) has responded to the elongate shape of the reptiles it eats by becoming a highly elongated snake. The diamondback rattlesnake (*Crotalus adamanteus*) has responded to the large girth of its typical prey by evolving into a snake of great girth itself: its broad head and flexible throat region enable it to do what even the largest bushmaster

could never do, namely, swallow an adult cottontail rabbit (*Sylvilagus* sp.), which exceed 1000–2400 g. Similarly, the thickset gaboon viper, which at 1.6 m (and 10 kg), can feed on animals the size of adult opossums (*Didelphis marsupialis*; pers. obs. in captivity). The evolution of a large predator usually coincides with large food requirements; yet, for some reason, in the bushmaster this trend has become reversed. We reach a strange paradox, for here is the world’s longest viper balking at swallowing prey that even a much smaller *Bothrops asper* (at less than half the body weight) has no trouble taking (see Table 8).

What do bushmasters normally eat? Any small mammal or bird within the given size threshold. The rice rats (*Oryzomys* spp.) and spiny rats (*Proechimys* spp.) would appear to be the most typically eaten prey in the wild (deduced from presence of spiny quills and undigested mandibles excreted in the stools of wild-collected snakes; pers. obs. in Surinam, Panama, Costa Rica and Atlantic Forest Brazil). H. Greene removed an *Akodon* sp. from the gut of a museum specimen of *L. muta*; he removed a whole *Oryzomys* sp. and the hind legs of a *Proechimys* sp. from another (source USNM holding records of *Lachesis*). Wild-caught bushmasters that will not take laboratory rats (*Rattus norvegicus*) in captivity will often readily accept spiny rats, as well as squirrels (*Sciurus* sp.), probably due to a similarity of scent. One could argue that spiny rats present the ideal prey size for the frequent-feeding, small-prey-size-consuming bushmaster: the rodents are slim, lithely built,

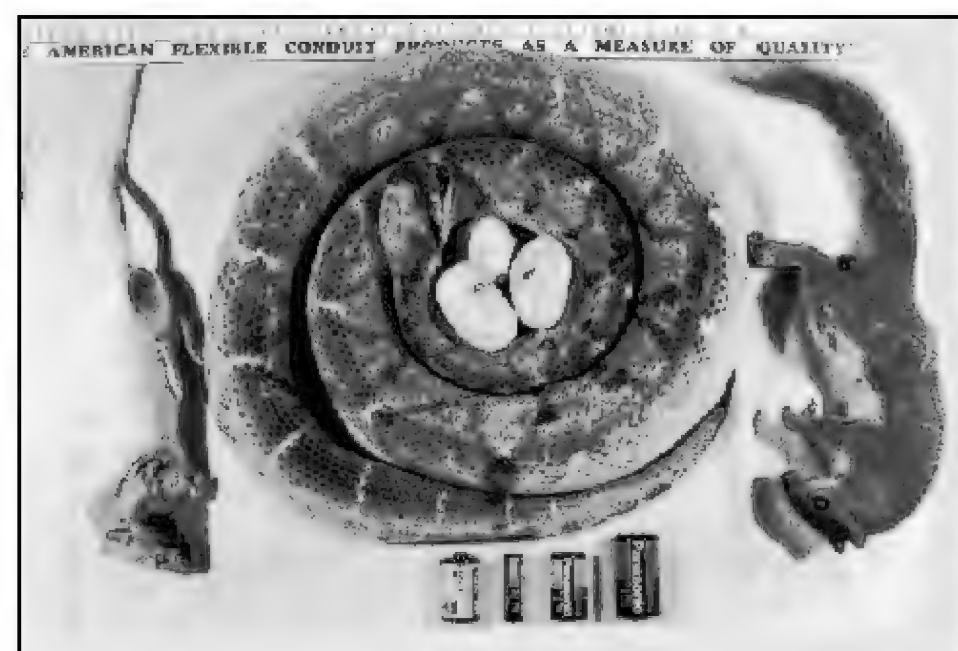


Figure 19. Adult bushmaster alongside typical maximum-size prey items. This wild-caught male snake lived in captivity for 12 years, attaining a weight of 7 kg. In no instance would it swallow prey exceeding the size of these sample prey animals, both 400 g. The largest prey size that has ever been engulfed by any of 40 large adult wild-caught bushmasters at the author's facility was a prey animal of 595 g, or about 6% of a 10 kg snake. However, the snake could not digest the huge meal and regurgitated it five days later. Relative swallowing capacity (i.e., the ratio of maximum prey weight to snake body weight) is greater for young bushmasters than for adults. This is true of nearly all snakes; however it is more extreme in the bushmaster. As the bushmaster approaches maturity, the ratio of prey size to snake size drops more rapidly than in other snakes. Accounts in modern scientific literature of adult bushmasters swallowing 40–50% snake body weight prey items (e.g., Boyer et al. [1995]) are fanciful. Pound for pound the adult bushmaster probably has the lowest prey size swallowing threshold of any snake species. (Note: eggs in center are frozen bushmaster eggs that did not hatch; batteries indicate relative size of the adult snake compared to neonates and sub-1-year-old examples shown in Figures 15–17.)

with most of the body girth concentrated in the haunches, making them easier to swallow (the hind limbs can be engulfed one at a time). The overall weight of a spiny rat is seldom more than 300–380 g, although occasionally one may reach 500 g (Nowak, 1991). This fits perfectly within the adult bushmaster's prey size threshold. Perhaps bushmasters have evolved their low prey threshold, special hunting tactics and morphology, merely to meet the prey size demands posed by this kind of prey alone, and that, with an abundance of this food item available, the snake, once reaching its adult size, has no pressing need to compensate by developing a larger prey threshold. Yet it is undeniable that bushmasters attain great size. . . . If the small spiny rat is the main food supply, why get bigger?

The limits of snake-design are described in Table 8, where we look at the less specialized (and one might say, more successful) morphology of *B. asper*, which gives it a broader choice of prey, and habitat. To recant an significant phenomenon, the prey size swallowing threshold of bushmasters little increases once a bushmaster has reached its normal adult size. Thus we observe a 3 m bushmaster only marginally capable of swallowing prey of greater dimension than what a 1.7 m bushmaster is capable. While the bushmaster is very seldom selective as to the size of the prey animal it will kill, it is highly selective about what size prey it will swallow. Girth of the prey item, weight of the prey item, with duration of the swallowing attempt, would seemingly trigger the acceptance or refusal of the meal. How frequently the keeper observes the partially swallowed, disgorged and rejected meal swallowed *only to the shoulder region of the prey animal* and not beyond. It is as though the snake has somehow quantified the size of the prey merely by taking it in its mouth, and elects by some unknown criteria either to complete the swallowing process, or abort it.

This phenomenon is now being noticed by other keepers of bushmasters. Randal Berry, a reptile keeper at Little Rock Zoo, in Arkansas, has a large private collection of bushmasters of two species. When I explained to him my prey size findings, he supplied the following personal communication, which closely parallels my own experience:

As per our discussion, the *L. stenophrys* I have in my collection are around 6.5 ft in length and weigh 12.5 and 13 lbs each. They are fed according to shed cycles, and fed thawed dead rats. They are fed weekly. The rodent weight is approx. 285–350 g each. Larger rodents, as you know, can weigh in excess of 500 g! When attempting to feed the snakes rodents of 400+ g, the snakes usually reject it. I think they know the meal is too large, so they will not eat it. The 400+ g rodent is swallowed up to the shoulder region and then regurgated.

A 12 lb snake weighs 5448 g. So, a 25% [snake-body-weight] food item, at that percentage, would weigh 1362 g! I have not attempted to feed a bushmaster a food item of 25% of its body weight, because (1) it would not eat it, and (2) I would be wasting my time and a food item.

It is my opinion than an adult specimen of *Lachesis* will reject rodent prey of 500+ g, being too large to manipulate and swallow, and thus the feeding process will always be aborted.

Mr. Berry's snakes, it is worth mentioning, are wild-caught examples and not related to my own stock. (He does not note the obvious difficulty of finding a laboratory rat exceeding 1300+ grams! At 25–30% snake body weight, one wonders what sort of monster rodents Boyer et al.'s [1995] seven three-year-old bushmasters were eating at 7-day intervals in their study, in order to "stay hungry"!)

There are some very good reasons why bushmasters use discretion in consuming large prey. In Andrade et al. (1997), we observe digestion as an "energetically demanding" activity in the rattlesnake *C. durissus*, "with an estimated cost equaling 12–18% of the ingested assimilated energy." However, adult *C. durissus*, which has no trouble swallowing and ingesting prey above 30% snake body weight (pers. obs. in captivity), is a dweller of very hot and dry habitats. While rarely necessary for rattlesnakes in countries like Costa Rica, basking in sunlight is a readily available option to thermoregulate and thus help facilitate digestion of prey (basking becomes important for the rattlesnakes in southeastern Brazil, which has a quite cold "winter" season; pers. obs.).

The bushmaster, by comparison, endures consistently cool conditions for a large ectotherm, living in rainy, cloudy mountain versants whose ground surface rarely sees sunshine. In the diurnal shade habitat preferred by these snakes; temperatures may barely exceed the low 20s C. Not only is ambient temperature some 10–15°C cooler than for *C. durissus*, basking in sunlight is less an option for bushmasters owing to the hydration needs of its skin, prone to dysecdysis unless kept continually moist. In the damp conditions of the pluvial forests, dysecdysis can evolve into a potentially life-threatening condition. An ulcerative dermatitis develops beneath the unshed skin.* Perhaps for this reason, bushmasters seldom bask in sunlight and generally avoid exposing themselves to it for any considerable length of time. The bushmaster is largely dependent on available ambient temperature in order to regulate its body temperature, in conditions generally of diurnal shade.

Large prey is more difficult to digest than small, requiring greater time, at a greater expense of energy, and while the returns are great, they are worthless if low temperature causes poor digestion that in turn provokes regurgitation. My data show a much higher incidence of regurgitation of incompletely digested prey (as opposed to partially swallowed prey, which has been discussed) when the "overfed" bushmaster has consumed single large prey items than when several smaller prey items totaled equal mass. Temperature is an important cofactor in digestion of prey in bushmasters, as in other snakes. A much higher rate of regurgitation of prey occurs in reduced temperatures (20–22°C) than in median temperatures (23–27°C). Experimentally, it is possible to induce regurgitation in bushmasters simply by lowering the ambient temperature for as little as 2–3 hours within the 3–5 day period after the snake has fed. A bushmaster having taken large prey would likely find it more difficult to digest at lower temperatures (and at a greater expense of energy); and in many cases may be constitutionally unable to do so. And how much greater the expense of energy

* Upon necropsy the lesions have been found to contain the bacteria *Stenotrophomonas mallophilia* and *Flavobacterium odoratum*, complicated by a fungus, *Trichophyton terrestre* (Ripa, unpubl. data).

to kill, recover, swallow, and attempt to digest a large prey item only to have to regurgitate it before digestion can take place, thus necessitating yet another hunting sequence, recovery, swallowing, etc., gambling against temperature and prey size in order to acquire an ingestible meal! Thus a “safe bet” for prey taking would be to take small prey frequently rather than single large prey items, given the environmental parameters inhabited by these snakes. In the cool temperatures of the diurnal shade habitats, the low prey size limitation is a fundamentally more successful option for digestion of prey.

And yet, if an eater of small prey, why did the bushmaster become such an elongate snake? If *Ophiophagus hannah* grew longer in order to eat *longer* snakes, and *Bitis gabonica* became enormously thickset with a broad head in order to eat massive hyraxes (*Procavia* sp.), then why did the spiny-rat-eating bushmaster grow long, but with low girth, and a comparatively very small head? A good way for evolution to circumvent the digestive problems posed by the low temperature habitat, and yet compensate with a maximum diversity of prey amount (but not size), would be to develop a very elongate, somewhat slender snake, with an elongate digestive tract capable of digesting large numbers of small prey. Recall our earlier finding: that the prey size threshold of a 2.5 m bushmaster is not substantially greater than that of a 1.7 m. example. The size increase of almost one meter has not significantly increased the dimensions of the snake’s head, nor its ability to engulf large prey. However, the 2.5 m bushmaster, having gained little in the single mass of what it can swallow, has gained enormously in the number of prey items it can consume at a time.

An interesting parallel can be observed in *Atropoides nummifer*, the jumping viper. This heavy-bodied, mesic-forest snake looks like a bushmaster “shrunk down” and compressed to the girth of a sausage. It is also a strike-holder like the bushmaster (Chiszar and Radcliffe, 1989). But if anything, the jumping viper inhabits even cooler elevations than the bushmaster in Central America, “taking over” in those cloud forest elevations where the bushmaster “leaves off” (although occasionally their distributions will overlap). The ground surface in cloud forest seldom sees sunshine, and precipitation is almost continual. Owing to the difficulty of trailing the prey on a frequently inundated ground surface, strike-release would be a less successful prey getting strategy than strike-hold. The jumping viper, like the bushmaster, does not have a very toxic venom to rodent prey (Bolaños, 1982). And the jumping viper’s squat physical build would make it poorly suited for trailing prey, which could escape to distances of several meters before succumbing to the effect of the venom (pers. obs. in captivity). (Accounts of prey trailing in viperids are recorded in Brock, 1980; Estep et al., 1981; Hayes and Galusha, 1984; Chiszar and Radcliffe, 1989). Ecologically, the jumping viper is in much the same predicament as the bushmaster: how to catch, swallow *and digest* large (or large numbers) of prey at temperatures lower than for most large ectotherms. But whereas the bushmaster has circumvented this problem by increasing body length (and so its digestive tract), the jumping viper has increased its digestive abilities by evolving into one of the stockiest bodied snakes in the world. It has solved the problem of digesting prey at cool temperatures by increasing the volume of

its stomach laterally, while the bushmaster has increased its stomach volume longitudinally. Note that an adult jumping viper at 100 cm is capable of consuming prey size equal to that of a 2 m bushmaster (pers. obs. in captivity).

So we see that limitations posed by temperature may have influenced not only the low prey size thresholds of bushmasters, but also the very size of the snake itself. The bushmaster did not evolve into a large snake in order to engulf large prey (if it had, it would have evolved a large head, and very elastic jaws and throat such as in *B. asper*); if it had, the prey size capacity would increase as the snake’s body length increases, which it does not do after it reaches a specific adult size. *Rather, the bushmaster evolved into a large snake in order to be able to digest more prey of a low size threshold at temperatures suboptimum for most large ectotherms.* The greater the body length, the more rodents it can consume and digest at suboptimum temperatures. Its reliance on diurnal shade habitat, its greater abundance at median elevations (above 100 m; see Table 5), and a physiological inability to make much use of basking to enhance prey digestion—these contingencies have required it to become a more efficient in digesting prey at lower ambient temperatures. And unlike the *Bothrops* forest vipers, which frequently bask; or the boids, which consume very large prey and are long-term baskers in sunshine, the bushmaster’s large size is compromised by needs of adequate concealment. The larger boa constrictor (*Boa constrictor*) can take to the treetops to digest its meal; the smaller *Bothrops* can hide almost anywhere, and because of its light weight is an excellent climber. But the large adult bushmaster, which when coiled may displace a ground area equal to that of small automobile tire, has little choice but to seek a burrow underground, or a large hollow log. Indeed, it is exactly to such cool dark places that the bushmaster retreats after having fed.

Yet there is a disparity. For assuming the consumption of large prey mediated by temperature, how does this relate to the young or neonate bushmaster, which, as we have seen, can consume relatively large prey for its size? Neonates inhabit the same elevations and habitats as adult bushmasters. . . . Why has temperature (as regards digestion of prey) in diurnal shade habitats limited the swallowing capacity of adults much more than it has the young snake?

One does not have to look far for the answer: From the same physical principle by which a *cup* of cold water will warm much more quickly to room ambient temperatures than will a *basin* of cold water; or by which a single ice cube will melt much more rapidly than a bucket of that same ice. After the cooler night temperatures during which these snakes typically feed, the large ectothermic reptile may not in the course of many hours of daytime temperature achieve a thermally viable level for successful prey digestion, while the smaller neonate can warm quickly to ambience in much less time. By the laws of thermodynamics, the adult snake at high elevations must then subsist at a generally lower body temperature year round than the young snake. Its general feeding threshold will be maintained at a lower level.

All this is verifiable by the fact that a bushmaster (or any snake) maintained at lower temperatures will grow much more

slowly than a bushmaster maintained at higher temperatures, owing to a slowed metabolic rate and thus slowed digestion of prey, resulting in a reduced capacity to feed. Prey digestion at higher temperatures is less energetically demanding, and the result will be more efficient prey digestion, and more frequent feeding, translating into greater growth size. Thus there are no very large ectotherms found in cold environments, and only the Boelen's python (*Morelia boeleni*) has reached subalpine elevations through possessing a jet-black exterior color and an habitual use of basking in available sunlight during the morning hours (pers. obs. in Irian Jaya). But the option of basking, comparable to that done by the python, is not viable for the bushmaster, owing to the lesser availability of sunlight in the diurnal shade habitat, and to the specialized hydration needs of its skin. The limits of habitat have shaped these vipers to a degree of specialization outside of which they cannot survive.

Strike-hold behavior

As with prey size, strike-hold capacity is ontogenetic; being proportionately greatest in neonates (which can achieve 30–40% snake body weight). The ratio of strike-hold prey size to snake size decreases as snake size increases, becoming evident when the snake reaches the 80–90 cm TL, 500–700 g body weight, range. Strike-hold “failures” occurred when (1) prey exceeded a weight threshold (see Table 4, “Strike-hold prey size capacity”) and when (2) a “poor hold” was obtained on the prey animal, which involved retaliation of the prey. Dead prey could be strike-held at a much higher weight threshold than live prey: thus it was possible to induce a strike-hold sequence in a dead rodent of 400 g when not even the largest bushmaster could (or would) manage prey of this weight while it was living and struggling. “Ambivalence to feed” was another contingency, but instances where items were not consumed were not included in order to qualify strike-release as hunger induced and not random or defensive. In a successful strike-hold the prey animal is nearly always seized at the midbody or anterior body portion of the prey animal; when seized posteriorly the prey is nearly always released.

The concept of strike-release in bushmasters is problematic, since bushmasters do not seem to employ this as a facultative strategy but always from failure to attain “good” strike-hold. If the prey is too large to strike-hold it may be too large to eat and is not always chemo-trailed. Bushmasters appear to have a nearly instantaneous awareness at the moment of strike contact whether to maintain their grasp on the prey or to release it, according to size threshold and/or the retaliatory advantages of the prey. Such awareness corresponds with some ideas presented in Boyer et al. (1995). However, Table 4 introduces actual snake body weight vs. prey weight data (Boyer et al. [1995] offers only percentage rates), and shows a difference in use of strike-hold between Central and South American forms (as was suggested in Ripa [1994]). Moreover, Table 4 factually challenges Experiments II and III of Boyer et al. (1995), since by my data oversized and uningestible prey items (“25–30% of snake body weight” for seven examples of three-year-old bushmasters) were presented to the snakes in Experiment III (approx. prey weight deduced from percentage rates of snake body weight given with respect to ages of the snakes,

compared against other three-year-old *L. muta*). In the Boyer et al. (1995) study of two- and three-year-old snakes, all prey offered would have been outside the capacity of the snakes either to strike-hold or swallow, since any bushmaster exceeding 2000 g in weight would at 25–30% snake body weight have had to consume a rodent that surpassed the prey-size ingestion threshold for the largest bushmasters in captivity. A normal three-year-old *L. muta* should weigh not less than 2500–3500 g, making a “25–30% snake-body-weight rodent” about 625–875 g in weight. Not even the largest bushmaster of 10 kg can consume a rodent of that size. Boyer et al. (1995) not only have their three-year-old bushmasters swallowing these gigantic prey items, but they have them doing so on a weekly basis in order to “stay hungry” for the next experiment!

“This procedure,” reads the text, “ensured that each snake ate during each trial, keeping hunger constant (i.e., snakes were always ‘7 days hungry’ at the start of each trial).” Faced with such massive and uningestible food, a strike-release sequence would have been *inevitable in every case*, and facultative use of strike-release over strike-hold could not then be proven since no snake would have been able to eat the meal as they claim. Because Boyer et al. (1995) offer no hard data, only percentage rates, readers are left to deduce the actual prey weights vs. snake body weights for themselves. And yet how to find an acceptable middle ground for ingestible prey from the information given? To increase the size of the snakes is to increase the size of the percentage weight meal, in other words, one comes up with ever larger and ever more uningestible prey. To do the opposite (reduce the size of the snakes), will reduce prey size, and be compensated to some extent by ontogenetic differences in the prey size threshold, but there are limits as to how far we can credibly “shrink” a three-year-old bushmaster till it begins to look suspiciously like something other than a three-year-old. Even if we grant these workers the freakish, that somehow their three-year-old bushmasters were only about 1200 g (normal *L. muta* of this age are over 3000 g) — in other words, that at three years of age they did not exceed the size of my own nine-month-olds (or their own 16-month-olds, as recorded in Boyer et al. [1989]); and this in spite of an evidently observed ability to consume gigantic meals of over a fourth their own body weight so as to “stay hungry” from week to week during the experiment — their prey at 25–30% snake body weight (300–360 g) is still well beyond the prey size capacity of snakes of that small size to strike-hold and consume (300–360 g prey can but marginally be strike-held even by many large adult bushmasters exceeding 2 m and 5000 g, and only presentations of *live prey* are admissible as representative of strike-hold capacity as it occurs in nature). A two- to three-month-old bushmaster at 200 g could conceivably swallow a prey item of 40% its weight (80 g); and while it is remotely conceivable that a six-month-old, 90 cm bushmaster at 500 g could swallow a prey item of 40% its weight (200 g), it is not probable that the latter snake could have strike-held it (experiments to repeat this have all failed). Nor is it probable, given the observed low prey size digestion thresholds of bushmasters, that the larger snake could digest the prey item before it turned to poisonous carrion. The snake that ate such a meal must either perish with the indigestible mass inside it or be

forced to disgorge the rotten matter. Probably the great size of the mass, swelling up with gas in the animal's esophagus (only the head and anterior body portion of the rodent would fit within the snake's stomach) would prevent the reptile even being able to disgorge the meal successfully, and a lethal action would follow in any event. Since the best test of the accuracy of any experiment is to replicate it, may I say that I have not, after considerable attempts, been able to replicate the experiments posed by Boyer et al. (1995). In no case has any bushmaster above 1000 g been able to strike-hold 25–30% its own body weight, or to swallow it—much less the 40–50% posed. The problems and inconsistencies presented by that article lead me to doubt the accuracy of its data and thus its conclusions.

Activity and concealment

What is the “normal” activity of bushmasters? As in all snakes, activity consists of the enactment of specific survival routines. In bushmasters, these routines involve maintaining a specific site of concealment, from which the snake will emerge during hours of darkness in order to feed and drink, afterwards returning to the concealment place before daylight. Significantly, the hunting site of bushmasters is usually distinct from the site of daytime concealment.

The type of concealment preferred by bushmasters has been verified by various reports from the wild. Mole (1924; also in Ditmars [1910]) and Ripa (1994) report taking bushmasters from the underground burrows created by paca (*Agouti paca*) and armadillo (*Dasypodidae*); local informants claim they frequently find bushmasters in these underground channels while excavating the mammals (armadillo is routinely eaten in rural areas and paca meat is considered a great delicacy all over Latin America). With the help of local hunters, the writer has excavated bushmasters from such burrows, and upon occasion, multiple bushmasters from the same burrow (bushmasters will congregate within such burrows, especially during the breeding season; one male and two female bushmasters were taken from such a burrow, as described in Ripa [1994]). Mole (1924) describes a man being bitten by a bushmaster while inserting his hand into such a burrow. There is anecdotal evidence of cohabitation of the snakes with the burrow-making mammals, all being too large to be considered prey (Ripa, 1994).

Paca burrows may be located in banks, on slopes, among tree roots, or under rocks, and usually have one or more escape routes (Nowak, 1991). Structurally, they are simple tubes of approx. 20–40 cm diameter, extending to a length of 3–6 m or more. (Paca burrows are often significantly devoid of vegetation at the main opening, with the ground surface usually denuded 1–2 m around the burrow mouth; owing to the traffic [and perhaps feeding] of the mammal; the main entrance to the burrow is often situated on a hillside in a sunny place, and sunlight warms the opening of the burrow to some extent. It is here that bushmasters, especially *L. melanocephala* and other bushmasters of high elevations, probably do some limited, or indirect, basking. A photo of such a burrow containing a bushmaster can be seen in Ripa [1994]). When occurring in relatively level terrain, I have found the burrows to run parallel with the ground surface usually at a depth less than 40 cm.

Hunters trail the paca to the burrows using dogs, and the hunters I have traveled with had no trouble excavating the paca using only the machete as a digging tool (i.e., the tunnels were not deep beneath the ground, but only long and circuitous). Bushmasters could also be excavated in this way, provided the burrow could first be determined to have a bushmaster inside. (Excavating paca burrows at random in the hopes of finding bushmasters can be a very unrewarding endeavor!)

In one case I was able to lure a bushmaster (*L. melanocephala*) out of the burrow simply by swaying my body repetitively in front of it, “snake charmer” fashion. The “cornered” snake followed my movements with its head, then, after some minutes, it rushed out quickly as though to chase its adversary away. In fact the “chase” proved merely incidental to an escape tactic, for the snake then continued along its course at considerable pace over the edge of a hill. (It proved to be a male upon capture. Females more typically stand their ground regardless of circumstances; males often flee.) Examining the burrow afterwards, I found it to be no more than about 1 m deep. Because of the shallow depth, the snake could not make good its escape, and elected to leave the burrow rather than stand its ground within. Thus, an important feature of a “good” burrow would appear to be that it possess enough depth for the snake to be able withdraw well inside it in order to escape from enemies.

Bushmasters that have a choice between lying out in the open under available plant cover during daylight, or the use of secure dark underground cover will almost always choose the burrow. Bushmasters seem oriented to the burrow, even more than to the feeding site. This reliance on the burrow site can be observed in captivity. Here, safely hidden, the snake spends 90% of its time, even when kept for long periods without keeper contact (the snakes being observed through a blind). To remove the snake from its burrow, and offer it no comparable concealment place, has the effect of disorienting the animal. Upon removal, it immediately begins searching for the burrow. If unable to find it, the snake lies about in the open or under available secondary cover; however, the normal processes of ambush hunting, breeding or combating are all interrupted until a burrow site is restored to it. Predatory and reproductive routines are evidently reliant first upon successful concealment.

Given a simulated habitat that meets certain environmental parameters (including near darkness in a burrow, simulated by black plastic 30–45 cm diameter PVC pipe, 2 m deep, filled with an earth or peat moss substrate, and partially submerged within another earth-simulating substrate; large crawl space for nightly exploration, diurnal shade answering for daylight, adequate humidity, availability of water and introduced live food) the wild-caught captive bushmaster will revert to normal “wild” behavior, and begin performing typical bushmaster survival strategies, including regular feeding, breeding and combating. Indeed, the need for the burrow as “home base” is so entrenched in bushmaster behavior that the keeper has found that in acclimating large wild-caught adult bushmasters to captivity, he had only to provide a set-up offering the above parameters in order to achieve what most zoos have had trouble accomplishing since the days of Ditmars: that is, take fresh-

caught *adult* bushmasters from the wild and have them feeding within a few days of captivity (and even more remarkably for a bushmaster, have them breeding within their first three months). If the snake believes itself to be “in the wild,” it will behave as though in the wild. The requirements of “wild” obey simple but precise guidelines that once fulfilled “reproduce” the wild state from the standpoint of the bushmaster.

How does the bushmaster find its way back to the burrow? The spatial orientation skills of bushmasters have not been studied, but there is evidence that the snake leaves its own chemical trail. Ripa (1994) devised a simple experiment based on removal of “home burrows” and relocation of those burrows, in order to see which burrows the snakes would favor. Even in large enclosures bushmasters had no trouble relocating their burrow sites provided the old chemical markers were allowed to remain (that is, the old mulch or moss substrate was not removed during cleaning). But the substitution of various “fresh burrows” that had not contained bushmasters previously (and thus no bushmaster scent) even in the identical location, showed a lower success rate of recovery. The chemical clues lacking in the new burrow kept the bushmaster searching until it found its previously used burrow, even though that burrow had been moved to another location within the enclosure.

Thus, the bushmaster’s spatial sense is probably formed to some degree by chemical associations, as is observed in the chemical trailing of prey. It is not farfetched to think that the lingering chemical trail of the burrow-digging mammal itself (whether paca or armadillo) could assist the snake in finding its way back to its lair in the wild, or help it to locate new such lairs; but this interesting area is completely unexplored.

Providing a “home burrow” is integral to instigating the normal feeding routines of wild bushmasters in captivity. Consider the behavior of the acclimated wild-caught adult bushmaster that is moved to a novel enclosure containing no burrow and no familiar chemical markers. Deprived of the sensory cues by which it enacts its strategies spatially, it lies about exposed on the ground surface, going “nowhere” from having no “place” to go (*place* being defined chemosensorially in relation to the hiding site). It enters a state of lethargy and torpor. Formerly a frequent feeder; now it loses all interest in food, and only “comes alive” for a few hours after dark when it begins exploring, either to escape the enclosure or in an effort to find a new burrow (burrow, from the standpoint of the snake, being equated with escape and “wild”). Note the frequency with which it returns to the same site to coil after the nightly exploratory crawl—the site where it most detects its own scent. If no burrow (or other secure hiding area) is provided, and this situation is allowed to continue, a “maladaptation syndrome” supervenes, often irreversible. After some weeks, even if a burrow situation is offered to the snake (in an attempt to induce it to begin feeding again), the snake will not try to find it. Having already given up feeding, now it has given up hiding as well. The snake wastes away and eventually dies. The failure of most large zoos to maintain bushmasters alive as display animals testifies to this phenomenon.

An observer who has seen such starving bushmasters in captivity, lying in the same place week after week exposed on

the floor of the terrarium, and making no attempt to defend themselves when confronted by the keeper, will assume these to be the most supremely sluggish and docile of snakes. The radio-tracker, having surgically implanted a transmitter in the snake’s body cavity, and then released the snake to a novel locale (or to the identical locale where it was found, albeit after the snake’s chemical markers have dissipated) will observe a similar phenomenon, only one more complicated by the lengthy convalescence that will take place after the surgery (the stress induced “benumbment syndrome” described by Ditmars (1910). In both cases the animal will evince a sluggish character, but this is not due to the natural temperament of the snake; rather it is undergoing a form of sensory deprivation (due to a lack of specific sensory cues) and exposure due to inadequate concealment.

In acclimating wild-caught bushmasters I have found it effective to introduce the new captive into an enclosure that has previously been inhabited by other acclimated bushmasters, that is, one that retains the substrate containing their chemical markers. The newcomer then orients itself to these chemical markers, has no trouble establishing itself in the home burrow (also containing the chemical markers) and takes up there in routine fashion. Soon it is exhibiting the same normal patterns of nightly emerging, crawling, and returning to the burrow before daylight, as its fellows. It begins feeding. It may even breed within a few months of captivity, providing it is little disturbed.

If the lodging offered is dark and secure, the captive bushmaster will adjust more readily. Hence a PVC pipe that was white in color was not effective, but a black one was. The bushmaster will usually retreat to the point furthest from the opening, where it is darkest, and remain there during the daylight hours. It is always at the extremity of the burrow that the eggs are laid.

While the subterranean niche seems best suited to the needs bushmasters, a “good” burrow can also be a hollow log situated aboveground, a site in which I have also found bushmasters in the wild. Some disadvantages of the hollow log site are proneness to flooding, infestation by ants, termites, and other insect pests, and presence of various fungi, all of which could be damaging to eggs. As such, I doubt that hollow log sites are used by these snakes to deposit their eggs.

Underground concealment is not only the choice of bushmasters when it is available to them (as is demonstrated repeatedly in captivity), its use is the soundest of all survival strategies in the wild. Lying out in the open or under plant cover is very poor survival tactics for a rainforest snake. In normal undisturbed rainforest conditions it might well end up being made a meal of by peccary (fam. Tayassuidae), probably the bushmaster’s greatest natural enemy. That bushmasters are often found lying aboveground and exposed, or under mere surface plant cover, is not evidence that this is where they predominately lie, rather it is symptomatic of where they are most commonly encountered by human beings: the fact that one can walk for weeks and even months in primary forest without ever seeing a bushmaster (or other snakes) is an indication that subterranean concealment is the predominate conceal-

ment (it is not an indication of a scarcity of bushmasters, whose populations must be at least dense enough to support breeding pairs finding each other). Bushmasters found lying out during daylight, as they often are, between the buttresses of ceiba trees, etc., constitute secondary circumstances relative to man's own terrestrial contingency, not the snake's. Significantly, I have found bushmasters lying out on the ground surface, or had them brought into me by local informants who had also found them lying out, most often after a heavy rain of the night previous: the snakes would appear to have been flooded out of their burrows. The wildlife dealer of Surinam, Theo Henzen, who has probably taken more *L. muta* from the wild than any other person during this century (through the use of the bounty system), reports a similar observation: it is usually in the days after a very heavy rain that bushmasters are found by indigenous people (Theo Henzen, pers. com.). The bushmaster is perhaps not quite as rare a snake as is popularly imagined, but the choice of its concealment, and its nocturnal habits, would make it appear so.

Another feature of the burrow is that it can serve as a secondary hunting site for the snake, for any suitable prey that wanders into the burrow will be taken (small prey mammals like echimyids regularly using existing underground burrows as nesting sites; Nowak [1991] and pers. obs. in captivity). In captivity bushmasters often lie in wait for prey to enter the burrow, so it evidently must constitute a viable although probably secondary strategy. In any event, the most predation likely take place not within the burrow but along the small mammal runway where prey can more dependably be found (the frequency of bushmasters *emerging* to hunt once prey scent is provided them in captivity, would support this). Thus, at some point the bushmaster must usually leave the burrow to hunt a meal.

Departure from the burrow is not a matter of the snake suddenly "waking up and leaving." It is a gradual and sequential process. During the last hours of daylight, *L. melanocephala* (using this species as an example) begins to stretch its body out to full length within the burrow, surveying the opening in characteristically elevated head stance (the head may be held upraised to some 20–30 cm above the ground surface just beyond the margin of the burrow opening). Here the snake may remain positioned for a period of 20 minutes to several hours, alert to signs of movement, or chemical and heat indicators that will tell it whether it is safe to emerge. If the "coast is clear," the snake will emerge entirely, and form an ambush-hunting coil at a proven-effective hunt site (or explore in order to find a novel hunt site). In the wild, it would seem important that the snake not travel too far from the burrow, for the burrow must be relocated when hunting is over, and often on very damp or even inundated terrain, increasing the difficulty of relocating it by chemo-trailing. (Recall the greater frequency with which bushmasters are found lying out in the open after heavy rains. Have they lost the chemical markers that enable them to relocate their burrows?). The exploratory crawl to find the hunt site, and the taking of the ambush-hunting coil, may be done on a nightly basis if the snake is in the feeding cycle. It will be repeated until enough food has been taken, afterwards returning to its burrow/lair for a period of inactivity

during which it digests the meal. This inactive period varies according to the size of the meal. If the meal exceeds 6–8% snake body weight in the adult bushmaster, it may not hunt again for 7–14 days; if the meal is below 6%, it may continue to hunt nightly).

As stated, a hunt site is a small mammal runway where the bushmaster will take its prey. Such a hunt site can be simulated in captivity by introducing live rodents into the large enclosure on a regular basis, and providing feed stations for them; the rodents will usually follow the chemical clues of other rodents along a specific runway to food, water and any provided shelter or nest site. The bushmaster will detect this area and make it a "feeding site" to which it will return again and again to get prey. (Greene and Santana [1983] associate the feeding sites of bushmasters with *Welfia* palms; the palms produce seeds which rodents eat. This is undoubtedly true; however, the sheer abundance of *Welfia* palms and all forms of food for rodents to eat in rainforest areas would make it unrewarding to look for these or other rodent feeding sites in order to find bushmasters. The palms are literally almost everywhere, and the bushmasters are nowhere to be found!)

Judging from available food supply for rodents in rainforest, suitable prey for bushmasters must be plentiful, and so the likely first requirement of bushmasters is not hunt sites (which are common) but effective concealment in large animal burrows (which are not common). The estimated population of adult paca, for instance, is no more than about 38–54 adults per km² (Nowak, 1991). And finding a "good hunt site" is to some degree taken care of by the burrow-building mammal itself, which will usually construct its burrow near to a vegetable food source anyway (Nowak, 1991; and pers. obs.). The food needs of the herbivorous *Agouti paca* are not dissimilar to those of typical bushmaster prey, the echimyids (see below).

The ambush coil is typically crotaline, and may be described thus: From the coiled position, the snake extends its head and neck in a horizontal line to a height of about 2–3 coils. The neck is held rigid, and angled slightly to a level above the dorsal head. The impression is of a steel spring wound taut, an effect contributed to by the sharp and angular dorsum of the neck, bent into a sinuous "S." The snake is keenly attentive to chemical or heat input, and the slightest motion of a warm bodied (but not a cold bodied) object will provoke the head and anterior portion of the reptile to come gliding forward. The degree which the neck is extended varies according to the intensity or significance of the cues. A prey animal making its appearance at a distance too far to strike will provoke a lengthening of the anterior body, so that more "S" is thrown into the neck coils.

The bushmaster's predatory strike might more rightly be described as an "aerial attack" than the quick horizontal stab-release of other crotalids. Because of the snake's large size, the striking head has the aspect of "swooping down" on the prey. The bushmaster may "bob" its head rapidly just as it strikes in order to thermally "sight" the prey (a quick vibratory motion of the head, vertically or horizontally depending on the trajectory to be achieved, that is seen within a second of the strike). The strike is swift and almost unavoidable. It may

change direction at the last moment in order to accommodate change of direction in the prey. The target has been zeroed in on by a “heat-seeking missile” that is attentive to the continuously shifting coordinates of moving warm-blooded prey.

Once the prey is seized another maneuver quickly occurs. With a quick forward lunge of its anterior body (and often the entire body), the snake immediately upraises the prey to a height of 20–40 cm above the ground surface. The prey is held suspended in midair, with the jaws clenched tight and the fangs deeply embedded. This prompt head elevation prevents the prey dislodging itself from the snake’s jaws (in instances where prey elevation is not achieved, the deflection of violent struggling prey kicking against ground surfaces can be so extreme as to literally bounce the snake’s head about like a tennis ball). With the jaws clenched, the enlarged labials are projected upwards, protecting the eyes and heat pits from prey retaliation (Chiszar et al., 1989; and pers. obs.). Here the taut, powerful musculature, thick vertebral column with its fleshy anchoring (in the dorsal ridge), and strong lateral body compression (most evinced anteriorly), would appear to provide tensile strength in the manner of an overhead truss system for the vertical elevation/suspension of the heavy prey (Ripa, unpubl. data).

Another strategy, rather than holding the prey aloft, is for the snake to pinion the prey against the ground surface with great force. The snake’s neck conformation (reinforced by the pronounced middorsal ridge and strong anterior lateral body compression), again braces against violently struggling prey, and here the dorsal ridge can be observed visibly arched as it projects the downward-thrusting head. Probably no other snake has been so physically modified to enact the strike-hold maneuver as the bushmaster.

The prey may die within a few seconds from the venom and large goring fangs (which may exceed 3 cm), or live as long as ten minutes within the snake’s jaws. There are occasions when the fangs are not employed at all, and the rodent dies from the sheer constriction of the snake’s powerful jaws around its midsection. Once seized in this way, and strike-hold is ascertained as “successful” by the snake, there is very little that can induce the snake to release the prey animal. In captivity one can physically pick up the snake by the “handle” of the prey animal itself, lifting the snake’s entire body full off the ground on some occasions, without the snake letting go its future meal. To disturb the prey, or attempt to remove it from the snake, will only increase the tenacity of the hold, for the snake evidently reads movement of prey as an indicator that prey is still alive and only bites down harder. Once the prey has ceased moving entirely, it is released and repositioned for swallowing.

If prey flees prior to the strike, the snake may “pursue” the prey with the anterior body portion extended to a length greater than 60% of its total body length (with the posterior portion of the reptile remaining relatively fixed). Here the head and neck launches out in a gliding downward rush to “pluck up” the prey. Thus in a 2 m coiled bushmaster, about 1–1.2 meters of its length may be actively in motion to chase prey. If this is not successful, the snake may leave the coil entirely and commence a full pursuit of the prey. The final strike (as well as

the above described pursuit) appears entirely heat coordinated.

Such constitutes the primary predatory activity of the bushmaster (and thus most all its general activity when not engaged in reproduction). It is not the only method by which the bushmaster will acquire its prey, however. If hungry enough, the bushmaster will raid the nest site of rodents. It will overturn objects (or containers holding prey), and dig down into mulch substrate and pluck live prey out that has burrowed beneath shelter. Museum records (USNM 192284) provide an account of a *L. stenophrys* that was found “sitting on top of a trap containing a live *Oryzomys* [rice rat]. It is by no means confined to the ambush-coil strategy, but its use is the more usual. The frequency with which feeding is engaged (in the young fast growing bushmaster, which can take relatively large prey frequently; and in the adult bushmaster, which cannot take relatively large prey in proportion to its body size, and thus must also feed frequently), and the use of the burrow from which the bushmaster must emerge to do its hunting, drinking, breeding, combating, etc., demands a relatively active lifestyle for these snakes, seemingly greater than for comparable *Bothrops*.

The bushmaster is a highly active, aggressive hunter and frequent feeder by night, even as it lives a sedentary existence by day, relying on the deeper cover of underground passageways for concealment from enemies. The often violent reproductive rituals of these snakes have been described at length in Ripa (1994), and some of these, with the new description of the male combat ritual, are reviewed in Table 6. Together these characters provide a picture of the bushmaster more in line with Ditmars’ (1910) view of a snake “highly active for a pit viper” than with the view of modern herpetology which often depicts bushmasters as one of the most phlegmatic of snakes. The “sluggish, inactive bushmaster, lying out for weeks unmoving on the forest floor” probably has its origins in (1) observations of bushmasters encountered during daylight hours during the period of their greatest inactivity; (2) injured or maladapted captives that have been stressed by inadequate confinement or other unsuccessful husbandry techniques in captivity; or (3) the traumatized behavior of bushmasters that have been surgically or otherwise physically restrained in order to implant a radio transmitter (see Ditmars [1910] for a description of the typical “benumbment syndrome” that occurs when these snakes are restrained in order to be force-fed).

Bushmasters are very sensitive to all forms of stress and one might argue, one of the most difficult of all snakes to radiotag successfully. The snake, convalescing after its stressful “abduction” by human beings, may remain relatively inactive for the entire first month of the study while it heals itself from the surgical implantation of the transmitter. It may little move from the general vicinity where it has been released. Its movements are further limited by the loss of chemical markers in the now “novel” situation into which the snake has been placed. For once the snake recovers enough to begin enacting normal survival strategies and routines, the original chemical markers will have dissipated. (Provided it *does* recover. It may not, and simply drag itself about sluggishly for the duration of the study, eventually succumbing to secondary infections from the

wound in the continually damp forest environment. Medicating the snake during this period will little help matters, for any confrontation between the radio-tracker and the snake will induce a defense reaction that, characteristic of bushmasters, will further limit its movements). The subject specimen assumes the attitude of our aforementioned captive that had been removed from significant sensory cues and offered no satisfactory concealment place. Having no memory of how it got “where” it is and no chemical map to tell it “where” to go (treating chemical markers as “memory” of spatial coordinates: the literal map of the territory), and unable to “find” itself spatially, the return to normal behavioral patterns and routines (including finding a home site of concealment) is further delayed. In short, the entire first month to six weeks of the study will be thrown away waiting for the snake to recuperate from its surgery, then some further weeks required for it to re-establish its chemical markers so that it can again resume the normal survival patterns and routines (all involving chemical placement). Unfortunately, after all this time, the signal from the surgically implanted transmitter may already be getting feeble, and may soon require replacement! To do so, however, will only repeat the cycle, with even poorer performance the second time for the snake has already undergone the stress of one operation and may not be able to endure another. Even to capture a bushmaster from a certain burrow and then release it back within that same burrow (the best alternative to all this) is to wait for a considerable period while the snake heals itself from its difficult encounter with man and reorients itself to the burrow site and its typical strategies. The problematic bushmaster, at once the most secretive, sensitive, and specialized of snakes, remains an elusive subject for field observations involving radiotelemetry.

Of mice and men: the bushmaster lethality disparity

Gutiérrez et al. (1990) report that the venom of bushmaster neonates (at age 15–20 days) is almost “devoid of toxicity,” with lethality in mice “not achieved even at doses as high as 24 µg/g.” The venom “did not induce hemorrhage, myonecrosis or inflammation.” They speculate that newborn bushmasters have trouble killing their prey by venom alone and must strike-hold prey to compensate: “. . . prey immobilization is achieved mechanically, thereby making unnecessary the presence of toxic components for this particular purpose.” Having raised over 100 bushmaster neonates of three species over ten years, I have never seen a mouse (*Mus musculus*) survive a bushmaster bite even if it was strike-released—and the mice always died rapidly enough that they were easily trailed and recovered by the snake. While contradicting the Gutiérrez et al. (1990) study for mice, I can confirm low lethality for larger rodents (*Rattus norvegicus*) based on captive feeding observations. Young bushmasters do have trouble killing edible rats (>20% snake body weight) without the use of strike-hold, due to the bitten rat escaping to a distance farther away than the snakes could (or would) trail it (see section in text on “Prey Size and Predatory Frequency”). And as described earlier, adult rats that escaped the strike-hold attempts of adult bushmasters often survived long enough to completely avoid being eaten by the snake—some did not die for minutes or hours, and

others not at all. (By contrast, I have never observed a rodent to survive the bite of any *Bothrops* species). Rodents that survived bushmaster bite presented little necrosis and only one case of bullae (from the bite of *L. muta*) was seen. Even rats that were strike-held often survived for some minutes in the snakes’ jaws and in rare cases death did not occur until more than ten minutes had passed. There is no doubt that the “mechanical” aspect of prey immobilization is important to bushmasters of all ages (see section above on “Prey Size and Predatory Frequency”).

Based on my observations of neonates feeding (literally thousands of feeding episodes), I cannot understand the inability of the 15 sample neonates in Gutiérrez et al. (1990) to produce a toxic enough venom to kill mice. However, some good possibilities are: (1) Husbandry of the newborns may not have been consistent with the development of healthy offspring, and/or the snakes were malnourished at the time of the extractions. Indeed, the latter would be inevitable with a newborn aged 15–20 days. At 15 days none of hatchlings would have eaten their first meal, since 14–15 days is required for newborn bushmasters to have their first ecdysis. Only after the first ecdysis will feeding in these species normally begin. Thus the baby snakes would have already utilized almost all their remaining egg nutrients by the time the venom was extracted. Venom production is an energetically demanding activity (Andrade et al., 1997; however, little work has been done to determine the exact cost of it) and it follows that poorly nourished snakes would produce low venom yields and toxicity. (Bolaños [1972] reports venom yields of adult bushmasters falling from 233 mg to just 64 mg after being in captivity; probably the stress of extraction and captivity prevented these snakes from adapting and feeding.) Perhaps developing newborns require the digestion of a first meal in order to produce “healthy” venom. Once feeding, however, venom quality would probably not restore itself immediately as complete digestion of the first prey item would require an additional 14 days, and one must infer an interval to reconstitute the venom. Hence the venom of newborns might reflect a different toxicity if taken at an earlier or later date. But this was not done because (2) Venom in the study was not sampled continuously as the snakes grew, rather only at “15–20 days of age, and then at one and two years.” Thus, in consideration of point 1, if the initial sampling was done only at 15–20 days and not again for one year, an appearance of a graduating toxicity of the venom would naturally be inferred; being nearly devoid of toxicity in the early trial, it could only have been more toxic in the one-year-old and adult snakes. (3) Repeated extractions from newborns (to determine if the results were an artifact of sampling) were probably not practical since, given the sensitivity of bushmasters to stress, the handling required to extract venom would have undoubtedly harmed and probably soon killed them (neonate bushmasters die easily when subjected to stress). In any case, the snakes would have soon ceased feeding—if they had ever fed to begin with—and thereby wasted away. (4) Mice bitten by neonate bushmasters are usually injected to a depth of at least 8–10 mm (the length of the neonate fangs). With the compression exerted upon the mammal’s midbody (the customary bite site in strike-hold), venom is injected deep

into the body cavity and into the vital organs. The Gutiérrez et al. (1990) study consists of injections that are “intradermal, into the footpad, and i.m. into the thigh.” Only the thigh injection could qualify as a “normal” condition of bushmaster bite upon a mouse; however, such a bite would probably result in a strike-release as this “poor hold position” would give the prey a retaliatory advantage.

Turning from mice to human beings, I observe the following contradictions with the findings of Gutiérrez et al. (1990): The bite of a one-week-old *L. stenophrys* (occurring in 1993) on my thumb produced intense pain, edema reaching the elbow (that did not subside for 7–10 days), with the thumb sore and stiff for about 30 days. The wound was by one fang, probably not completely embedded. There was no bleb formation, and no necrosis. Here was clear evidence of the capability of bushmaster venom to produce inflammation in a human being, with certainly a lethal potential to mice.

Bite two (fall 1994) was a strike-hold bite resulting from a feeding response. The snake was a subadult captive-born and -raised *L. melanocephala* (TL 150 cm). The snake’s mouth closed across the knuckles and base of my ring finger, then *held on*. Despite a firm grip by the snake (I had to shake it off my hand), and the full embedding of one 2+ cm long fang into the tendinous area immediately behind the knuckles (the other penetrating to a superficial depth in the web of the fingers), the bite produced nothing more than intense local pain, a swollen hand and forearm (not surpassing the elbow), with a month of “stiff and sore” fingers. There was no necrosis. Here was a potential for life-threatening effects from a large snake with a definite intent upon killing prey, and yet clearly not much venom was injected. A witness to the bite remarked afterwards that “bushmasters must not be very poisonous.”

If the previous two bites would have given this impression, bite three was overwhelming evidence of the ability of bushmasters to kill, and kill rapidly, an adult human being. On 17 April 1995, a 120 cm *L. melanocephala* (subadult, nine months old) struck the ulnar aspect of my right hand, and gave what (from past experience with snakebites) I recognized within seconds to be a serious envenoming. Pain was immediate and rapidly spread from the bite site throughout the hand, into fingers and wrist. Since few readers can be familiar with what a bushmaster bite feels like, I can only compare the sensation to having your hand slammed in a car door—*repeatedly*. That goes double for a bite on the digit, where the pain is even more intense because more concentrated (with the distension of swelling this pain can become almost unendurable). As the venom spreads there is a deep burning throb that appears to be *ballooning* outward through the skin, as though the bitten area were being inflated from inside with a hot, corrosive liquid—there is a feeling of the flesh expanding. Which is exactly what is happening as the extremity begins to swell with fluid, blowing up to grotesquely distorted and unnatural proportions. Before four to five hours have passed, the member will have converted itself into something more resembling a cow’s udder than a human hand.

This bite was a feeding response with a brief strike-hold. There was considerable bleeding from deep fang penetration

(the fangs of a snake this size are roughly 2 cm). I took this bleeding to be a bad sign as there are two large veins running transversely in the ulnar part of the hand. An attempt to bleed the hand manually through the fang wounds (under cold running water to prevent coagulation) was fruitful, however of doubtful utility considering the depth of penetration. Swelling, which began after two minutes, soon closed off the wound openings and no further blood could be “milked” out.

Systemic effects were rapidly incapacitating. *At 10 minutes*: dizziness, incoordination and inability to stand; temporary losses of consciousness; altered sensorium (visions of hallucinogenic color patterns, sense of enlarged surrounding space); drowsiness with feelings of euphoria. *At 15 minutes*: nausea; sweating and cool skin; feeling of swollen tongue (making speech difficult); numbing of lips that accompanied uncontrolled drooling/alternately dry mouth and difficulty swallowing; pain in lymph nodes; rapid pulse (rising to above 110). *At 20 minutes*: projectile vomiting; loss of bowel control with diarrhea; increasingly rapid pulse (to 125); lowered blood pressure (91/54). *At 25 minutes*: continued vomiting and uncontrollable diarrhea; chills; violent upper abdominal cramping; intense burning pain in kidneys (lower back) and violent cramping in lower back; labored but rapid breathing (with a feeling of suffocation); falling blood pressure (67/51); rising pulse (130). *At 30 minutes*: continued upper abdominal and lower back cramping; vomiting and diarrhea; chest pain; cold ashen skin; blood pressure continuing to fall (48/35); difficulty breathing, like a weight on the chest. *At 35 minutes*: continued vomiting and diarrhea (I had collapsed on the floor, unable to crawl to the toilet); blood pressure falling to undetectable levels; pulse undetectable; respiratory distress; cyanosis of the extremities; red spots on face, neck and chest (without hives); general body numbness. *At 40 minutes*: No detectable blood pressure, no detectable pulse. Conscious but disinterested in fate.

EMS workers entered to find a “well developed 38-year-old white male lying on floor as if dead . . . wife says he has been bitten by a bushmaster snake . . . fang wounds unbelievably far apart, approximately 3 cm. . . . Patient somewhat sedated but oriented times three, cooperative, and able to give pertinent information . . . said he needed epinephrine and Benedryl, with additional doses of antivenom intravenously . . . had taken nine vials intramuscularly before calling EMS. . . .”

Actually, my wife called EMS. I would have been incapable of so much as dialing a phone number. Significant was a general body numbness while my wife administered, with a large gauge syringe needle, the nine intramuscular injections of antivenom (90 ml). “Okay, you can start now,” I told her, readying myself for the jabs—in fact she had finished minutes before.

Systemic effects continued in route to hospital and for some four hours more while in hospital. Oxygen was given, intravenous fluid, 50 mg diphenhydramine (Benedryl), epinephrine drip to control hypotension, along with 50 ml polyvalent antivenom intravenously (*Anti-Botropico*, *Crotalico*, *Laquesico*, produced by Instituto Clodomiro Picado, Costa Rica). Myoglobin and fresh-frozen plasma were given to help restore

fibrinogen. Symptoms fit the profile of hypovolemic shock due to decreased circulating fluid volume (Russell, 1983; Watt, 1989)—a condition which antivenom cannot restore. However, disturbances of the autonomic nervous system, leading to vagal stimulation, are also postulated to be the cause of such symptoms, a clinical picture compatible with neurotoxic poisoning (Haad, 1980/1981; Fan and Cardoso, 1995). The extreme rapidity of the symptoms, even before the extremity had much time to swell, makes one wonder if a radically *decreased* circulating fluid volume could have had time to occur.

Massive edema of the bitten arm to above the shoulder and involving the lateral upper chest and back, with considerable bruising, remained for some weeks, however, general recovery was rapid and without complications. There was no bleb formation and no necrosis. (For a more in depth description of the sequelae and treatment in this bite, an article is in preparation).

Yet another “opportunity” to observe the effects of bushmaster bite on man occurred in November 1998. This bite was from a neonate *L. stenophrys*, aged 2 months (TL 57 cm; Wt. 95 g) that I was manually assisting in a bad skin shed. An angry, strike-bite where the snake “held on” (unusual in a defense bite), it had to be violently shaken off, where it ripped free of the digit and fell to a distance of about 4 m away. The fangs had penetrated the soft fleshy underside of the second joint of the right index finger, through the muscle to the depth of the bone. Based on past experience, I was instantly aware of having gotten “another bad one.” There was considerable bleeding from the two wounds, with attempts to massage out as much blood as possible.

This bite was extraordinary in that so small a snake produced many of the systemic alterations seen in the previous episode. Intense burning pain in the kidneys and lower back began within 20 minutes. Vomiting and diarrhea began within 30 min. Pulse rose to above 130. Severe hypotension was again noted (63/50). Drowsiness, fever, chills, violent stomach and lower back cramping, respiratory distress, red spots on skin (without wheals or hives), feeling of swollen tongue, alternating drooling and dry mouth, difficulty swallowing, cold skin, etc.,. At no point was consciousness lost, nor were there the color-hallucinations of the previous severe bite. Sensorium remained clear, however the violence of the illness left me incapacitated and quite unable to help myself (thanks again to wife!). I declined use of antivenom, and injected 50 mg Benedryl instead (frequent vomiting prevented retaining it orally). Then I waited out the illness. Three hours of painful writhing from abdominal – lower chest cramping, respiratory difficulty, with intermittent vomiting and diarrhea—but after this time most of the systemic reactions (other than vomiting) had ceased. Surely here, in this neonate bite, was injected venom of enough quantity and toxicity to kill innumerable small animals like mice—within 30 minutes the bite had completely overwhelmed a 180 lb man!

Swelling to the shoulder gradually increased for the next 36–48 hours, becoming massive. The arm became completely immovable. This condition persisted for over 14 days. There was no bleb formation. No necrosis resulted. After four months the bitten finger still lacks “normal” mobility, but has

responded well to exercise.

Of these four “interactive” bites, both the third and fourth are consistent with the grave systemic alterations to be expected from bushmaster bite. The first and fourth bite clearly demonstrate substantial toxicity of the venom of neonates to humans. In none of the four bites, however, did necrosis develop. Even the fang wounds did not abscess and “rot out” as one is accustomed to experiencing in the bites of species possessing less dangerous but ultimately more locally degrading venoms.

By contrast a mere three-month-old, 38 cm *Bothrops asper* from Trinidad produced marked necrosis on the author’s left index. Swelling extended to the shoulder, persisting for some 2–3 weeks, rendering the arm unusable. After three weeks the swelling had receded to encompass only the hand. The finger remained tensely swollen and immovable for some six weeks, with continual pain. Necrosis consisted of two blistered patches about 1.5 cm wide, one on the ball of the first joint—where the fangs entered—and the other, a second hemorrhagic eruption not related to the fang wounds (swelling had caused the finger to split open) on the inner lateral aspect of the second joint of the finger. Permanent damage was avoided by protecting the necrotic areas from disturbance and *not* debriding or cleaning the fang wounds. Even the pain was different; the *Bothrops* bite like that of fire-burn, the bushmaster bite like that of a spreading contusion. Although deeply burning within the first hours, the local pain from bushmaster bite was more manageable, numbing to a dull throb after some days, whereas the *Bothrops* bite continued with a deep fiery burn for weeks, sensitizing the skin surface in places that appeared clear and unaffected by venom (in this case, the forearm and back of the hand). Other than an intense headache, however, there were no general body symptoms in the *B. asper* bite. Here, the radically different effect of these two fundamentally different venoms can be seen exhibited in a single human “test dummy.” One (the *Bothrops*) locally severe, the other (the bushmaster) systemically severe. The former leaves damage from necrosis, the latter does not.

These data confirm reports of rapid severe systemic alterations in bushmaster envenoming (Bolaños, 1982; Gutiérrez, 1995; Fan and Cardoso, 1995), but contradict reports of myotoxicity and hemorrhagic effects (Rosenfeld, 1971; Watt, 1989). Supporting the Gutiérrez et al. (1990) hypothesis of low myotoxicity, no myonecrosis resulted even though in all four cases venom was injected directly into muscular tissue. Contradicting Gutiérrez et al. (1990), edema and inflammation were considerable in the bites of neonate no. 1, and massive in neonate no. 2 (the author’s elbow swelled to a circumference of 40 cm from 26 cm within the first 12 hours, the hand becoming approximately three times normal size, with fingers completely unbendable and partially absorbed into the mass of the hand).

These data also contradict the Gutiérrez et al. (1990) hypothesis that “venom of newborn specimens is not highly toxic to their natural prey” and therefore “severe [envenoming] might not be the case in accidents caused by newborn *L. muta* [i.e., *L. stenophrys*].” Just as there is no appreciable inability of the snakes to kill mice, there seems to be no inability of newborn bushmasters to evoke dramatic systemic reactions in

humans. While I do not believe a newborn bushmaster capable of killing a healthy adult human (though probably it could kill a child), my own case with the seven-day-old bushmaster is ample evidence of venom toxicity in newborns, and their ability to cause dangerous sequelae in man. By contrast, I do believe that an older neonate such as the two-month-old bushmaster described, is well capable of killing an adult. I have no doubt that the bite of a nine-month-old bushmaster of 120 cm (bite no. 3) could be rapidly fatal to an adult without speedy anti-venom treatment and supportive therapy (although technically not a newborn such a snake is still some two years away from being sexually mature). Probably many cases of rapid death from bushmaster bite attributed to the fangs striking a blood vessel result from just such hypovolemic shock episodes (or neurological alterations, if decreased circulating fluid volume can be shown not to be the cause) as are described in bite two. Rapid death from bushmaster bite would seem to result from the venom's ability to cause severe life-threatening hypotension within a short period of time.

Despite contradictory evidence to Gutiérrez et al. (1990), the two neonate bites do confirm their idea of bushmasters becoming more venomous as they grow—although whether it be due to venom toxicity or yield is less easy to determine. All four bites confirm low myotoxic and hemorrhagic effects of Central American bushmaster venom when injected into humans, as in mice. I believe that lack of necrosis and hemorrhage to be the two most important factors differentiating Central American bushmaster bites from *Bothrops* species (see below). The effects of *L. muta* bite are less clear, but here also I suspect some misunderstanding prevails within the literature.

Bite by *Lachesis* or *Bothrops*? How to tell the difference

Difficulty in identifying the species in snakebite cases has long been a problem in managing symptoms of dangerous envenomings. Killing or catching the offending snake is not always possible or practical, and can increase the likelihood of further bites. Some species, like the terciopelo (*Bothrops asper*), are quick to escape, and frequently the snake is not seen. While polyvalent antivenoms simplify treatments in most viperid envenomings, there are significant variations in symptomatology that can help identify the species, thereby aiding management and treatment. Here I compare envenomings from the two most venomous snakes in Central America, and show ways to distinguish between them when the snake has not been seen or has been misidentified.

Statistically, bite by *Lachesis* offers low morbidity but high mortality in all parts of its range (Bolaños, 1982; Gutiérrez et al., 1995; Hardy and Haad, 1998). *Bothrops asper* bite offers low mortality, but (as with all *Bothrops*) an overwhelmingly greater bite incidence (Gutiérrez et al., 1980). And yet there is a disparity. For as Hardy and Haad (1998) note, "... venom yields and LD₅₀s from the laboratory suggest that the terciopelo is potentially more lethal than the matabuey [bushmaster, *L. stenophrys*] in terms of an individual human envenoming. . . . [The bushmaster has] a proportionally smaller head and venom gland (pers. obs.), smaller initial venom yield (233 mg) . . . [lower] maximum yield of 407 mg (Da Silva et al., 1989) and

lower i.v. venom toxicity for laboratory mice (LD₅₀ 5.6 µg/g in mice)." The authors conclude, "The lesson to be learned is that mice are not human beings. the variation in susceptibility to snake venoms makes extrapolation of LD₅₀s from one species to another an exercise in futility."

There is no doubt a great deal of truth in this idea. And yet the statistical artifact itself may be responsible for the disparity. Statistics implicate *species* in snakebite morbidity, but they rarely consider the *size* of the snakes involved. The reason may lie not in the greater deadliness of the bushmaster *per se*, but in the greater size of the bushmasters that usually bite humans (i.e., large bushmaster = large fangs and large amount of venom vs. neonate or small bushmasters which have less lethal potential; see below).

Based on venom yield and laboratory toxicity, it seems probable that if bites by large 2+ m terciopelos were the predominate occurrence rather than the rare, the mortality rate for these snakes would equal if not surpass that of the bushmaster. Extrapolated from tests on rodents (Minton and Minton, 1969), a large terciopelo possesses enough venom to kill 20 or more adult humans (up to 1530 mg; Bolaños, 1982). Like the bushmaster, its fangs may exceed 30 mm, so the chance of these huge hypodermic teeth striking an important blood vessel is great.

Most snakebites in Central America happen to agricultural workers while laboring in the field, with 50% of all bites occurring on bare feet (Bolaños, 1982; Gutiérrez et al., 1995). These are likely bites by small snakes that are not seen and thus stepped on. But a two-meter-long snake as big around as a man's arm is conspicuous and rather easier to avoid. Based on accounts recorded in the literature (Hardy and Haad, 1998), I have noted that most all bites from large bushmasters involve the lower extremity, but not the foot (these snakes are capable of striking 40–50% their body length; pers. obs.). Inferring bites by comparably large terciopelos to be not dissimilar, leg bites would also predominately occur, putting these in the 18% category of "bites involving the lower limb." But neonates or small terciopelos would probably always bite the feet, or, when occurring on the upper extremity, hands (32%)—probably from individuals putting their hands directly on the snakes whose small size and camouflage has rendered them unseen. Deductively then, we can arrive at a rough guess that about 82% of bites (50% foot bites and 32% hand bites) are caused by small snakes, probably examples below 100 cm in length. Although no doubt error-filled, this interpretation suggests that statistical comparison of bushmaster bite to terciopelo bite is something of a rigged game. Probably for every one bite by a two-meter-long terciopelo there are *several hundred* bites by examples less than 100 cm long. During the three to six months succeeding the birth season, which occurs in September through December (Solorzano and Cerdas, 1989; and pers. obs.), this ratio is likely even higher, with the majority of offenders of even smaller size, < 50 cm (estimations based on my own collecting data, see below). Here we are talking primarily in terms of agricultural bites, since these form the bulk of morbidity statistics. But large terciopelos, like bushmasters, are quickly killed out of agricultural areas, their large

size making them a conspicuous target. Owing to their typical confinement within primary and secondary forest situations, these large serpents would logically be uncommon in snakebite incidence. And yet such bites no doubt occur. How often they do occur is not known—only a review of individual cases can tell us that. Based on my own limited data, I suspect that of the approx. 600 patients treated for snakebite in Costa Rica every year (20 per 100000; Gutiérrez, 1995), fewer than 5–10 individuals are bitten by large adult *Bothrops* of comparable proportions to the average adult bushmaster. Just where these few individuals stand in relation to the mortality figures is not known. However, it would seem logical that in those bites involving adults and not children, most of the mortality figures could be culled from the bite incidence of the larger as opposed to smaller snakes.

This is not to underestimate the seriousness of bushmaster bite vis-à-vis terciopelo (this can scarcely be done!), but to explain that, unlike terciopelos, neonate or young bushmasters are rarely implicated in accounts of snakebite. (A single account exists of a “juvenile” bite, but the snake’s actual size isn’t specified and even its identity cannot be positively confirmed; Torres et al., 1995). If neonate and “juvenile” (< 100 cm) bushmasters could be injected into the statistics to the extent of neonate and subadult (< 100 cm) terciopelos, the morbidity figures on bushmaster bite would undoubtedly be altered. This is not likely to happen, for baby bushmasters not only rarely bite people, they are rarely encountered in the wild (pers. obs. during wide-scale collecting activities in Panama, Costa Rica, Ecuador, Surinam, Guyana, and Brazil: see Ripa (1997) for an example of methods; pers. com., F. Furtado, Instituto Butantan; pers. com., Theo Henzen, reptile dealer, Surinam). Producing only six to 12 young annually that must be hatched in primary forest situations (bushmaster), compared to 60+ offspring a year that can be born *anywhere* (terciopelo), then the disparity of bite incidence between these two species is not hard to account for. In bushmaster literature we are left primarily with accounts of snakebites by adult snakes, and almost no bites by small or baby snakes. As in collecting, where it is the large adult (2+ m) bushmasters that are most often encountered, it is the adult bushmaster bite that has found its way into the statistics. Based on my own data using the “bounty system” in six Latin American countries, resident collectors typically brought me approx. 30 adult bushmasters to every neonate, all taken from primary forest. By contrast, in Costa Rica and Panama I generally received from 30 to 40, < 100 cm terciopelos taken from agricultural areas to every one 2 m terciopelo taken from agriculture and/or primary forest. During the birth season, these figures could jump to 100:1. Even if newborn or small bushmasters did often bite people—if they were abundant in agricultural areas and near people’s homes like terciopelos, instead of being confined mostly to primary forest—the chances of them being described statistically is small, because the tendency would be to absorb these bites into the greater morbidity of *Bothrops* and related genera (see below).

Here we must factor in another variable—that of mistaken identity. Consider the confusion occurring between *Bothrops asper* (and *atrox*) and all other venomous ground vipers in rural

Latin America. Whether the bite is by one of the *Porthidium* species, or any other potentially less lethal species, the easy handle is to blame it on the locally better known terciopelo (or its *Bothrops* variants). Indeed, few rural Costa Ricans (for example) bother to distinguish between the less venomous “tamaga” (*Porthidium nasutum*) and the terciopelo. One is simply the “baby” of the other. Hence an enormous number of bites attributed to terciopelo may be by the little (mostly inoffensive) tamaga.

Local confusion is more qualitative when extended to the bushmaster. For instance, once a terciopelo reaches or exceeds approx. 2 m, it automatically becomes a bushmaster in the popular mind. “Matabuey” (cow killer) and “cascabel muda” (silent rattler) and other local names for the bushmaster can denote *any large viper* of the proportions of the bushmaster. For example, when some years ago I put out a bounty for live “matabuey” in rural areas near primary forest, I was disappointed to receive almost all terciopelos (large ones) until my collectors (and in turn *their* collectors, for they were quick to make a business of it) learned to tell the difference. Thus, as far as the local people were concerned, to be bitten by a large terciopelo was to be bitten by a “matabuey.” And yet to be bitten by a small bushmaster was to be bitten by a terciopelo! (Baby bushmasters usually brought to me by native people were usually called terciopelo or “tamaga”). In effect, to many residents there were no small bushmasters, only terciopelos; there were no large terciopelos, only “matabuey.” Evidently, the only requisite for a snake being called “matabuey” (“cow killer”) is that it be big enough to kill a cow! I have encountered similar phenomena in all parts of the bushmaster’s range when I have put bounties out on venomous snakes. Even in Amazonian South America, where *B. atrox* is not a comparably large snake, local collectors often managed to confuse the two if the snake exceeded a certain size.

This indicates the amount of confusion that can occur statistically when one begins asking local people what bit them. As for the physician who sees the case, he may be left only with the symptoms to make a “positive” identification. Which brings us to the main point of this section.

In any case of severe envenoming attributed to bushmasters in Central America the telling factor can be summed up by one word: *necrosis*. If the victim experiences extensive blistering or blackening of local tissue, or any hemorrhagic effects (such as bleeding of the gums), the bite is assuredly that of the terciopelo. If the local damage is limited to massive swelling and muscle contracture, the bite is by the bushmaster. Systemic alterations such as hypovolemic shock (or disturbances of the autonomic nervous system, if this is what they authentically are; see previous description) are definite signs of bushmaster envenoming. Although there is no doubt that the bite of a large terciopelo *could* produce these same systemic effects and *as rapidly*, inevitably with such grave sequelae there must accompany *some* visible blood incoagulability (hemorrhaging of mucus membranes) and there must follow *some* necrosis. Indeed, postulating such a severe envenoming from a terciopelo that it would produce rapid systemic alterations (of the order of the bushmaster) is to postulate concomitant necrosis and hem-

orrhage, probably of massive proportions. In terciopelo bite, telltale bullae will form on the bitten extremity within as little as 2–4 hours and usually before 12 hours (Fan and Cardoso, 1995); the bite site will always be black and if presented as dark blue or purple will soon turn black. The bite wounds and surrounding areas will blister. But there is little or no blistering in bushmaster bite. Here the bite wounds may appear bruised, but they are basically clear and will not rapidly necrotize, if at all. The limb may swell to massive proportions—it may give the appearance of bursting.* If blood escapes beneath the skin (ecchymosis) it will be due to the pressure of edema, less than from degradation of the blood vessels by the venom. If sufficient antivenom is given soon enough there should develop little or no skin surface discoloration other than bruising; but not so with *Bothrops* bite, where the blood from ruptured blood vessels always turns black, having a hemorrhagic or necrotic contents. The fang wounds of the bushmaster may turn dark purple (in *Bothrops* they will turn rapidly black), and there may be a serosanguinous discharge, but no true hemorrhaging from the wounds will occur as does in *Bothrops*. With sufficient antivenom given in bushmaster bite, the fang wounds will rarely abscess (unless complicated by infection); in *Bothrops* the fang wounds will turn black regardless of antivenom treatment and will always abscess regardless of infection. A “scorched blackened limb” growing hard with necrosis and covered with bullae is not from the bite of the bushmaster—it is the hallmark of *Bothrops* bite. Myonecrosis is probably always due to bites by large *Bothrops* where the long fangs have delivered the potent myotoxin deep into muscle. With bushmasters the damage is usually limited to contracture, but the muscle does not necrotize (except from secondary contaminates). From this one can see that the majority of all Central American bushmaster bites (and perhaps South American bushmaster bites as well, although here the symptomatology is less clear) where severe necrosis is reported in spite of antivenom, have either been cases of mistaken identity, or the result of secondary infection. Contamination of the bite wounds with resulting complications can present a convincing impersonation of venom necrosis to physicians inexperienced with the effects of snakebite. Sadly, this has resulted in many unnecessary surgeries—if surgery can ever be said to be appropriate in an early treated snakebite.

Contradicting Watt (1989), who reports “severe local necrosis [in bushmaster bite]” surgical debridement is *never* indicated under any circumstances in the bite of the bushmaster, if that surgery is intended to relieve a supposed “venom necrosis.” Even in *Bothrops* envenoming, surgery is useful only when managing gangrene (never to be confused with venom necrosis) which usually requires days to manifest itself. Watt’s (1989) remark, “Careful, prompt surgical management is the key to minimizing damage in cases complicated by necrosis” is in fact the key to achieving disfigurement and mutilation. Although I find Watt’s (1989) advice generally excellent, surely worse advice was never uttered than this call to prompt surgery when dealing with necrosis.

Excising, opening (to drain), or surgically tampering with the bite site and surrounding areas *increases* necrosis and results in further degradation of the bitten extremity. The black, dead tissue covering the bite wound (in *Bothrops* bites) and surrounding areas must be left undisturbed—this veil of dead hematose flesh, no matter how gruesome looking, will grow hard and dry as the weeks progress, protecting better than any hospital bandage the compromised underlying tissue, and promoting its healing and regrowth. Necrosis is in essence a kind of “scab,” being composed largely of dried blood and blood extravasated tissue. Cut or tear it off and the exposed damaged tissue beneath it will infect and necrotize. Leave it alone and this dead material will slough off on its own, and new restored skin will appear. However, this sloughing process will not usually begin until swelling recedes and/or the new skin is ready (30–60 days). One must not yield to the impatience of expecting an immediate cure; nor should one yield to the persuasion of helpful physicians anxious to “do something” when doing nothing is the better course (often done only to satisfy the expectations of the patient). But such “blackened limbs” as these will not be seen in bites of *Lachesis* species—here the danger is not from necrosis, but from infection and tissue suppuration. (Note Bolaños [1982] where in three cases of death from bushmaster bite there was little necrosis [confined to a small area around the fang punctures in one patient] no organ hemorrhage, but with massive infection and tissue suppuration. Deaths resulted on the third and fifth day in spite of antivenom treatment—probably from an insufficient quantity of antivenom administered [patients received only 10 vials each; a fourth patient who received 20 vials, survived]).

As of this writing the author has endured 9 venomous snake bites, including envenoming from *Atractaspis* sp. (with necrosis), *Causus* sp., *Porthidium* sp., *Bothrops asper* (with necrosis), a 5 kg. 150 cm *Agkistrodon piscivorus* (requiring 14 days hospitalization and a year’s therapy to regain use of the hand) and four bites by two *Lachesis* species. Yet he is typing this manuscript with all 10 fingers, and in all cases but one he has healed without scarring (this single case involved the clinical lancing of a fang wound; the other wound, not lanced, healed perfectly without a scar). Had “prompt surgical management” been performed one wonders how many fingers—or limbs—he would have left!

Perhaps the danger with the advice given in Watt (1989) and others is the vague non-specificity of their terms: “prompt surgical management” and “complicated by necrosis” are just malleable enough statements as to be without practical meaning. Does “prompt” mean in regard to how soon the victims presented themselves to the physician, or how soon after the bite has occurred? Doctors naively following Watt’s (1989) advice will have no idea what “prompt” means in regard to necrosis and debridement—and begin cutting dead flesh away almost as soon as it manifests itself. *There is no reason to remove the dead tissue at all—it is already dead and if kept dry*

* I have endured edema so tense that even to twitch the fingers or elbow was to cause the skin to split open. Nevertheless, I believe fasciotomy to relieve pressure of swelling is never indicated. It causes permanent scarring, increases likelihood of infection and advances necrosis. The dangers of “compartmental syndrome” are probably overrated. Watt (1989) notes that “tense edema in the bitten limb rarely leads to vascular compromise.”

is *harmless*. It does not harbor or retain venom—at least, being dead and non-vascular it cannot further transmit venom to the underlying tissue. The compromised, living, and growing tissue beneath it surely cannot benefit by additional exposure to oxygen-eating bacteria.

“Complicated by necrosis” elicits only the vaguest judgment call—in fact, what seems to be implied is that the necrosis itself is the “complication.” Does the writer mean complicated by infection? Then treat the infection. Does he mean complicated by gangrene? Gangrene and venom necrosis are two completely different conditions, and should be treated as such. Gangrene spreads, having an origin not in venom but in bacteria. Venom necrosis becomes rapidly inert—the poison that has caused it will have already completely irrigated the tissue well before the attending physician sees the case. What then is the “complication” of necrosis that necessitates “prompt surgical management?” We must assume in cases where days have elapsed before the patient has sought medical help, where antivenom has not been used (or after its use is no longer efficacious), or when poor first aid measures (such as tourniquets or cryotherapy) have been employed resulting in damage secondary to the venom. Perhaps here—and only here—is surgery indicated. But the working physician, who may have never even seen a snakebite, will not have the least clue what “prompt surgical management” means when presented with a person’s limb turning rapidly black. He will imagine necrosis to be a spreading, out-of-control thing that must be cut out immediately or the patient perish.* Through the process of successive excisions I have seen cases where misguided surgeons have effectively “whittled” down potentially healthy appendages (that could have healed) to crippled, useless nubs.

The recent case of an agricultural worker and part time “snake hunter” in Costa Rica (a friend of mine whom I shall simply call “M”) is a testimonial to this. Bitten by an adult bushmaster on the forearm, and though receiving prompt antivenom treatment (200 ml), he had the misfortune to be clinically mutilated afterwards—a fasciotomy to relieve the “pressure of edema” and a massive excision to remove what *posed* to become necrosis but was in fact only the bruising of envenomed and severely swollen tissue. *The tissue had not even had time to necrotize before it was excised!* Indeed, there is no reason to believe it *would* have necrotized. The result was a gaping 16 × 9 cm crater cut to the depth of the muscle, in a largely ruined appendage that has required over a year in

skin grafts to restore, and will likely never again regain “normal” function. Thousands of cases like M’s occur every year in Latin America, Asia, Africa, and even the United States—victims of “prompt surgical management.” One doctor in Surinam told me that he routinely performed fasciotomies on every snakebite, and this usually entailed excision of the entire bite area as well! How many mutilations had this one doctor committed in his lifetime on patients who might have been better off trusting the local witch doctor! Ultimately the responsibility must lie with those medical authors who continue to recommend such practices in spite of mounting evidence to the contrary, or who use hastily concocted or vague terminologies that provide no clear idea of the diagnostics and indications of “taking up the knife.”

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* Cases of systemic myotoxicity even in severe cases are so rare as to be unknown, and usually no myoglobinuria is seen (Gutiérrez, 1995).

Table 1. Scale variation in three species of bushmasters, and one probable new species. Scale counts are given as the sample mean $\pm$ standard deviation, with the range below in parentheses; N is the sample size. All sources Ripa (1994) and Ripa (in prep.) unless otherwise noted.¹

Characters	<i>Lachesis muta</i>	<i>Lachesis stenophrys</i>	<i>Lachesis melanocephala</i>	Darien bushmaster
Ventral scales	221.8 $\pm$ 4.40 (213–230) N = 50	202.9 $\pm$ 4.90 (191–209) N = 40	213.6 $\pm$ 3.98 (209–222) N = 25	215.9 $\pm$ 4.40 (211–226) N = 11
Subcaudal scales	35.6 $\pm$ 1.40 (34–40) N = 50	39.7 $\pm$ 4.33 (35–49) N = 40	41.2 $\pm$ 5.48 (35–54) N = 25	39.5 $\pm$ 4.93 (35–53) N = 11
Dorsal scale rows at midbody	34.6 $\pm$ 1.32 (33–37) N = 50	34.7 $\pm$ 1.62 (33–38) N = 40	37.1 $\pm$ 1.34 (36–40) N = 25	34.2 $\pm$ 1.33 (31–36) N = 11
Supralabials	8.9 $\pm$ 0.90 (8–11) N = 50	7.8 $\pm$ 0.83 (7–9) N = 40	7.9 $\pm$ 0.88 (7–9) N = 25	9.4 $\pm$ 0.50 (9–10) N = 16
Infralabials	15.0 $\pm$ 1.11 (13–17) N = 50	13.4 $\pm$ 1.04 (12–15) N = 40	13.4 $\pm$ 0.96 (13–15) N = 25	15.1 $\pm$ 0.89 (14–17) N = 16
Rostral	Triangular, broader than high. ² Of reduced size between the large prenasals and narrower anterior head.	Triangular, as broad as high. Larger between the reduced prenasals and the broader anterior head.	As in <i>L. stenophrys</i> .	Triangular, large, as broad as high.
Prenasal scales	Enlarged, protuberant, triangular; with a dorsal face usually lower than the dorsal plane of the prefrontal area.	Reduced, flat, rounded, with a dorsal face lower than or level with the plane of the prefrontal area.	Reduced, flat, rounded, with the dorsal face level with or elevated above the plane of the prefrontal area.	Enlarged, protuberant, triangular; resemble those of Guiana Shield <i>L. muta</i> .
Internasal scales	Enlarged and distinct. Largest in Guiana Shield specimens.	Reduced, may be as small as the canthals and indistinct among the prefrontals. Clinal size increase east of Canal Zone, Panama, west of Chepo region.	Reduced, but never as small as in <i>L. stenophrys</i> .	As in <i>L. melanocephala</i> .
Canthal scales	Three. Elongated, distinct, raised (may form a slight ridge) in Guiana Shield specimens, becoming less pronounced in western Amazon specimens.	Three, infrequently two. Oval, flattened, and smaller than in <i>L. muta</i> , often hard to distinguish among the numerous small prefrontal scales, which may be the same size.	Three, infrequently two. Oval, flattened, distinct, larger than in <i>L. stenophrys</i> , they maintain their identity among the prefrontals.	Three. Oval, flattened, distinct, similar to western Amazon specimens and to <i>L. melanocephala</i> .
Postnasals	Single or divided.	Usually single.	Usually single.	Single or divided.
Preoculars	Two or three. ³ Relatively longer than in other species, in proportion to increased anterior head length.	Two or three. ³ Intermediate in length between <i>L. muta</i> and <i>L. melanocephala</i> .	Two or three. ³ Shorter than in other species, proportional to reduced anterior head length.	Two or three. Intermediate in length between <i>L. muta</i> and <i>L. stenophrys</i> .
Frontal and prefrontal scales	Large, oval, rugose; may form a ridge of 3–4 large knobby scales along the inner border of the supraoculars.	Small, fine, smooth; may be hard to tell from the canthals.	As in <i>L. stenophrys</i> ; however, always maintain their identity from the canthals.	As in <i>L. stenophrys</i> .
Shape of parietals	Elongated, triangular.	Oval or round.	Oval or round.	Elongated, triangular, as in <i>L. muta</i> .
Keeling of frontals and parietals	Increased.	Reduced.	Reduced.	Increased.

Table 1. (cont'd)

Characters	<i>Lachesis muta</i>	<i>Lachesis stenophrys</i>	<i>Lachesis melanocephala</i>	Darien bushmaster
Scale shape at midbody	Diamond-shaped mid-dorsally, as long as broad. In Guiana Shield specimens the scales usually retain this shape dorsolaterally, emerging from the interstitial skin in a U- or V-shaped line; the scales show little or no free apical portion. In western Amazon specimens the dorsolateral scales become more elongate, with increased free apical portions.	Diamond-shaped mid-dorsally. Become spade-shaped dorsolaterally, typically longer than broad, emerging from the interstitial skin in a straight line, giving the scale a half-round shape. This is in contrast to the usually diamond-shaped dorsolateral scales seen in typical <i>L. muta</i> . Conspicuous free apical portion.	As in <i>L. stenophrys</i> ; however, the scale is smaller.	Variably resembles <i>L. stenophrys</i> or western Amazon <i>L. muta</i> .
Dorsolateral scale size at midbody	Large, especially examples from the Guiana Shield.	Intermediate.	Small; up to half the size of comparable <i>L. stenophrys</i> . The interstitial skin is more distinctly visible surrounding the scale (to 1/4 scale width). Hence in an equal number of dorsal rows to other species, the scales will still be smaller in this species.	Intermediate.
Keeling in midbody scales	Increased (especially Atlantic Forest and Guiana Shield specimens), diminishing laterally; however, keeling on lower scale rows more prominent than in other species.	Reduced, diminishing laterally; lower scale rows usually smooth.	Reduced, diminishing laterally; lower scale rows less smooth than in <i>L. stenophrys</i> .	As in <i>L. melanocephala</i> and western Amazon <i>L. muta</i> .
Conformation of the keel in midbody scales	Tubular, with diminished width at the base. In Guiana Shield specimens, the keel is usually centered along the midline of the scale. In western Amazon specimens, may be shifted toward the apex.	Knob-like, less tubular, increased width at the base, becoming more obtuse dorsolaterally than in <i>L. muta</i> . The keel is usually shifted away from the midline of the scale toward the apex.	As in <i>L. stenophrys</i> .	As in western Amazon <i>L. muta</i> .
Conformation of the middorsal scale in cross-section, without the keel	Beaded, especially in Guiana Shield specimens. The scale is strongly upraised before the formation of the keel, and tapers little to the outer rim; the keeled portion of the scale rests on this already elevated surface, causing the scale to appear strongly embossed laterally, even when not keeled. In western Amazon specimens this character becomes less evident, with the scale generally flatter.	Flat, with a flat outer rim. The keel rests essentially on a flattened scale surface.	As in <i>L. stenophrys</i> .	As in western Amazon <i>L. muta</i> .

1. Other comparative data include: Solórzano and Cerdas (1986)—*L. stenophrys* (N = 54) ventrals, mean 203.3, range 198–209; dorsals, mean 35.0, range 33–38—*L. melanocephala* (N = 8) ventrals, mean 213.7; range 209–216; dorsals, mean 38.0, range 36–40. Peters and Orejas-Miranda (1970) summarize *Lachesis muta* as having 209–230 ventrals. Martínez and Bolaños (1982) provide scales counts for a single example of *Lachesis* from eastern Panama (*Lachesis muta muta*). These counts are: 226 ventrals; 53 subcaudals, 35 dorsals at midbody; 9 - 9 supralabials; 14 - 15 infralabials.

Table 1. (cont'd)

2. Campbell and Lamar (1989)

3. Note on preoculars. Campbell and Lamar (1989) remark three, while previous authorities remark two (Martínez and Bolaños, 1982; Solórzano and Cerdas, 1986). This is evidently due to a different definition of preoculars in relation to surrounding facial scales. Campbell and Lamar (1989) remark the second and lower preocular as forming “the upper and lower border, respectively, of the pit.” Using this definition, all bushmasters can be said to have three preoculars; however, this third preocular may not always be in contact with the border of the eye, so its usage is problematic.

Table 2. Structural variation in three species of bushmasters, and one probable new species. Measurements are given as the sample mean $\pm$ standard deviation, with the range below in parentheses; N is the sample size. Weight is in grams; weights were taken to the nearest 100 g. Lengths, widths and other distances are in millimeters. All sources Ripa (1994), and Ripa (in prep.) unless otherwise noted.

Characters	<i>Lachesis muta</i>	<i>Lachesis stenophrys</i>	<i>Lachesis melanocephala</i>	Darien bushmaster
Build	Elongated, more slender, with a lighter musculature and skeleton than Central American forms.	Moderately heavy bodied; substantially heavier musculature and skeleton than South American forms.	As in <i>L. stenophrys</i> ; heavy bodied.	As in <i>L. stenophrys</i> . These snakes attain considerable girth.
Weight	3360 $\pm$ 40 (2900–4200) N = 50	4620 $\pm$ 55 (3900–5400) N = 40	4216 $\pm$ 73 (3100–5600) N = 25	4940 $\pm$ 60 (4000–5600) N = 5
Lateral body compression	Reduced, with a round body conformation.	Increased, with a tall body conformation.	Increased, with a tall body conformation.	Increased, with a tall body conformation.
Body height at midbody	56.4 $\pm$ 5.01 (50–70) N = 50	73.8 $\pm$ 9.30 (60–89) N = 40	69.4 $\pm$ 10.44 (59–88) N = 25	77.2 $\pm$ 11.01 (62–80) N = 5
Vertebral ridge height at midbody¹	5.7 $\pm$ 0.92 (5–7) N = 50	8.5 $\pm$ 1.30 (7–10) N = 40	8.2 $\pm$ 1.40 (7–10) N = 25	8.7 $\pm$ 1.37 (7–10) N = 6
Head shape and size²	Smaller, thinner, relatively more lanceolate than Central American forms, especially in Guiana Shield specimens. Heads of western Amazon specimens tend to be larger, but retain triangular shape.	Large, blunt, becoming ovoid in adults.	Large, blunt, becoming ovoid in adults.	Shaped like western Amazon <i>L. muta</i> , but attains size comparable to <i>L. melanocephala</i> .
Head length, snout tip to posterior of mandible²	62.9 $\pm$ 2.95 (59–70) N = 50	77.7 $\pm$ 2.70 (72–81) N = 40	77.2 $\pm$ 4.09 (73–84) N = 25	75.2 $\pm$ 7.74 (70–85) N = 11
Head width at posterior of mandibles²	41.5 $\pm$ 1.87 (38–45) N = 50	46.8 $\pm$ 2.85 (43–50) N = 40	46.3 $\pm$ 2.43 (43–50) N = 25	45.9 $\pm$ 3.08 (42–50) N = 11
Dorsal head width at the frontal, anterior to supraoculars²	21.8 $\pm$ 1.49 (20–24) N = 50 Accounts for the arrow-like head conformation of this species.	27.6 $\pm$ 2.09 (24–30) N = 40 Accounts for the blunter anterior head aspect of Central American forms.	28.1 $\pm$ 2.24 (25–31) N = 25 As in <i>L. stenophrys</i> .	26.3 $\pm$ 2.41 (23–28) N = 11 As in western Amazon <i>L. muta</i> .
Distance from the anterior border of the eye to the tip of the snout²	20.8 $\pm$ 1.71 (17–23) N = 50 Because the overall head is smaller, the anterior head is proportionately longer.	20.6 $\pm$ 1.94 (17–24) N = 40 Reduced on the overall larger head.	18.8 $\pm$ 1.93 (16–22) N = 25 As in <i>L. stenophrys</i> .	19.7 $\pm$ 1.68 (17–22) N = 11 As in western Amazon <i>L. muta</i> .
Height of frontal region	Usually elevated above the level of the snout dorsum, so that snout appears sloping in profile.	May be level with snout dorsum or less elevated than in <i>L. muta</i> .	Unelevated; level or below the snout dorsum.	As in <i>L. stenophrys</i> .

Table 2. (cont'd)

Characters	<i>Lachesis muta</i>	<i>Lachesis stenophrys</i>	<i>Lachesis melanocephala</i>	Darien bushmaster
Height of supraoculars	Usually elevated above frontal.	Usually elevated above frontal.	Unelevated or weakly elevated above frontal.	As in <i>L. muta</i> .
Anterior surface of palatine bone	Variable; needs further study.	Straight. ³	Concave. ³	Insufficient data.
Venom toxicity in mice ⁴ (LD ₅₀)	37 µg/g s.c. (LD ₁₀₀) 30 µg/g i.m.	5.5 µg/g i.v. 6.2 µg/g i.p.	8.9 µg/g i.p. 6.0 µg/g i.p.	6.8 µg/g 9.8 µg/g Immunological comparisons show a close relationship to <i>L. melanocephala</i>

1. Measured from the fleshy ridge dorsum to the dorsal surface of the zygosphenes of the vertebra at midbody. Measurement taken by inserting a needle and measuring the depth of penetration.

2. Because of differences in head size in *L. muta*, there was a greater range in this species. Guiana Shield specimens scored lowest with the western Amazon specimens highest.

In *L. muta*, the posterior head often appears broader proportionally (but not actually) compared to Central American forms, suggesting an increased relative length of the quadrate bones (which dictates head width in many viperid snakes). Quadrate length in adult bushmasters usually ranges from 20 to 24 mm. Further investigation could prove this a meaningful diagnostic feature, however useless for external identification purposes. Mandibular length, which was also less in *L. muta*, was proportionately less reduced than anterior head width when compared with Central American forms. Other factors contributing to a more triangular appearance of the head in *L. muta* may be the usually more slender neck, which causes the head to appear more distinct, and more prominent venom glands, suggesting increased musculature in this area (the venom glands of bushmasters, like those of elapids, are largely covered by muscle [Pough et al., 1978]).

A word of caution in attempting head measurements of preserved specimens. Our predecessors have elected that we view bushmasters in terms of dentition. Consequently, the stiff, breakable specimens we find in museum jars have usually been fixed in grisly exhibitions of the spectacular long fangs. The normal outlines of the head are lost. The frontals are depressed and the posterior articulators widely dilated, with a variability in the latter of up to 15 mm. A thorough understanding of how bushmasters look when not in the “biting position” is recommended before such work is attempted.

3. Solórzano and Cerdas (1986); Greene (1997).

4. Schöttler (1951); Esquerre (1976); Bolaños et al. (1978); Gutiérrez et al. (1987); Hardy and Haad (1998).

Multivariate analysis comparing the Darien bushmaster to the three bushmaster species, *Lachesis muta*, *L. melanocephala* and *L. stenophrys*. The SAS System General Linear Model was used for the analysis. The multivariate analysis of variance (MANOVA) included the following 11 variables from Tables 1 and 2: ventral scale rows; subcaudal scale rows; dorsal scale rows at midbody; supralabial scales; infralabial scales; weight; midbody height; vertebral ridge height; head length; dorsal head width; distance from orbit to tip of the snout.

Hypothesis of no overall Darien bushmaster vs. others effect

Statistic	Value	F	Num DF	Den DF	Pr > F
Wilks' Lambda	0.56722870	7.2828	11	105	0.0001
Pillai's Trace	0.43277130	7.2828	11	105	0.0001
Hotelling-Lawley Trace	0.76295735	7.2828	11	105	0.0001
Roy's Greatest Root	0.76295735	7.2828	11	105	0.0001

Hypothesis of no overall Darien bushmaster vs. *L. muta* effect

Statistic	Value	F	Num DF	Den DF	Pr > F
Wilks' Lambda	0.30629562	21.6187	11	105	0.0001
Pillai's Trace	0.69370438	21.6187	11	105	0.0001
Hotelling-Lawley Trace	2.26481975	21.6187	11	105	0.0001
Roy's Greatest Root	2.26481975	21.6187	11	105	0.0001

Hypothesis of no overall Darien bushmaster vs. *L. melanocephala* effect

Statistic	Value	F	Num DF	Den DF	Pr > F
Wilks' Lambda	0.52958117	8.4791	11	105	0.0001
Pillai's Trace	0.47041883	8.4791	11	105	0.0001
Hotelling-Lawley Trace	0.88828468	8.4791	11	105	0.0001
Roy's Greatest Root	0.88828468	8.4791	11	105	0.0001

Hypothesis of no overall Darien bushmaster vs. *L. stenophrys* effect

Statistic	Value	F	Num DF	Den DF	Pr > F
Wilks' Lambda	0.57691844	7.0001	11	105	0.0001
Pillai's Trace	0.42308156	7.0001	11	105	0.0001
Hotelling-Lawley Trace	0.73334727	7.0001	11	105	0.0001
Roy's Greatest Root	0.73334727	7.0001	11	105	0.0001

Multivariate analysis comparing the Darien bushmaster to the three bushmaster species, *Lachesis muta*, *L. melanocephala* and *L. stenophrys*. The MANOVA was performed as above, excluding the variables of weight, midbody height, and vertebral ridge height, in order to have more data for Darien bushmaster (because of low sample size for these characters).

Hypothesis of no overall Darien bushmaster vs. others effect

Statistic	Value	F	Num DF	Den DF	Pr > F
Wilks' Lambda	0.64283809	7.9868	8	115	0.0001
Pillai's Trace	0.35716191	7.9868	8	115	0.0001
Hotelling-Lawley Trace	0.55560166	7.9868	8	115	0.0001
Roy's Greatest Root	0.55560166	7.9868	8	115	0.0001

Hypothesis of no overall Darien bushmaster vs. *L. muta* effect

Statistic	Value	F	Num DF	Den DF	Pr > F
Wilks' Lambda	0.40919475	20.7550	8	115	0.0001
Pillai's Trace	0.59080525	20.7550	8	115	0.0001
Hotelling-Lawley Trace	1.44382409	20.7550	8	115	0.0001
Roy's Greatest Root	1.44382409	20.7550	8	115	0.0001

Hypothesis of no overall Darien bushmaster vs. *L. melanocephala* effect

Statistic	Value	F	Num DF	Den DF	Pr > F
Wilks' Lambda	0.52654790	12.9255	8	115	0.0001
Pillai's Trace	0.47345210	12.9255	8	115	0.0001
Hotelling-Lawley Trace	0.89916244	12.9255	8	115	0.0001
Roy's Greatest Root	0.89916244	12.9255	8	115	0.0001

Hypothesis of no overall Darien bushmaster vs. *L. stenophrys* effect

Statistic	Value	F	Num DF	Den DF	Pr > F
Wilks' Lambda	0.47054428	16.1747	8	115	0.0001
Pillai's Trace	0.52945572	16.1747	8	115	0.0001
Hotelling-Lawley Trace	1.12519850	16.1747	8	115	0.0001
Roy's Greatest Root	1.12519850	16.1747	8	115	0.0001

Table 3. Color variation in three species of bushmasters, and one probable new species.

Characters	<i>Lachesis muta</i>	<i>Lachesis stenophrys</i>	<i>Lachesis melanocephala</i>	Darien bushmaster
Dorsal head pattern	Brown or black spots, in a geometric pattern. These spots may be large and distinct (numbering 6–20), or fragmented into numerous (over 30) smaller speckles, especially in Guiana Shield specimens, where they become less distinct.	Usually unspotted, or with a few small indistinct spots.	Uniformly black/blue-black, advancing dorsally from the postocular stripe, and including the nape middorsally.	As in <i>L. muta</i> .
Postocular stripe	Narrow in Guiana Shield specimens; broader in western Amazon and Atlantic Forest specimens. Whitish border above the eye stripe.	Broad. A lighter-than-ground-color hue (but not white) may border the eyestripe at the angle of the jaws, but this is rarely conspicuous.	Visible only in neonates, where it is separated from the black head-cap by a whitish border. A dimorphic trait of males, the neonate trait is sometimes retained, especially above the rictus.	Narrow postocular stripe (to half scale width in 30% of samples), with white border.
Amount of black pigment in the head dorsum ¹	Low in Guiana Shield specimens; high in western Amazon and Atlantic Forest specimens.	Low, but this species has a very broad black eye stripe.	Very high.	High.
Ground color	Orange tan, pinkish tan, umber tan. Orange in neonates.	Greenish tan to yellowish tan. Orange in neonates.	Deep yellow, straw yellow, cream tan, ivory; may be speckled with tan, dark brown, or black, especially posteriorly, where the scales may assume a “braided” appearance. Red orange in neonates.	As in <i>L. muta</i> .

Table 3. (cont'd)

Characters	<i>Lachesis muta</i>	<i>Lachesis stenophrys</i>	<i>Lachesis melanocephala</i>	Darien bushmaster
Middorsal blotches (shape and situation)	Rhomboid, with reduced vertical barring laterally; not extending into the ventrals except (infrequently) in western Amazon specimens.	Rhomboid, tending to vertical bars laterally; may extend into the ventrals in some specimens.	As for <i>L. stenophrys</i> .	As for <i>L. stenophrys</i> .
Middorsal blotches (color)	Brown, black.	Brown, black.	Black, blue-black.	Brown, black.
Middorsal blotches (number)	20–35	22–37	22–37	24–33
White or lighter-than-ground-color outlining middorsal blotches	May occur distinctly throughout.	Reduced, increasing posteriorly. In examples east of Canal Zone, Panama, may occur throughout.	May be present throughout; however, becoming more distinct posteriorly.	As in <i>L. melanocephala</i> and <i>L. muta</i> .
White or lighter-than-ground-color blotches along paravertebral line	Not conspicuous against the light ground color, these blotches are seldom white but merely a lighter-than-ground-color hue that will be fused with the light border outlining the dark dorsal blotches.	Conspicuous owing to darker surrounding ground color; may be cream-colored or pale tan. Three to five scale rows wide, stand out strongly as “points of light” along the spine. Posteriorly may merge with the light border of the dark blotches, but not anteriorly as in <i>L. muta</i> . Most distinct in this species.	As in <i>L. stenophrys</i> , but much less evident due to lighter, less contrasting ground color.	As in <i>L. melanocephala</i> .
Interstitial skin color	Tan to pinkish-tan.	Pinkish tan to greenish-tan	Pink, umber-tan, blue-gray, causing the relatively small, yellowish dorsal scales to stand out as though outlined. Like the scales, the interstices may be mottled with dark pigment, giving the dorsum a speckled appearance in some specimens, especially males.	As in <i>L. muta</i> .
Tongue color²	Red.	Red pink to tan.	Deep red, carmine, maroon.	Red to pinkish-tan.
Eye color	Red, brown, dark brown, with iris usually visible; bright in neonates.	Dark brown or black, obscure, iris usually not visible. Bright in neonates.	Transparent black, iris usually visible. Bright in neonates.	Red, brown, dark brown, with iris usually visible.
Subcaudals	Usually immaculate in Guiana Shield specimens; mottled in western Amazon and Atlantic Forest Brazilian specimens.	Always strongly mottled.	Usually immaculate.	Usually strongly mottled; immaculate in one specimen.
Dorsal tail-tip and tail-spine color	May be black or brown; usually light tan in Guiana Shield. Orange in neonates.	Usually black or dark brown in adults. Orange in neonates.	Usually black in mature adults, however, some examples, especially 1–2 yrs age, have a pale colored, yellowish gray, or even whitish tail-spine. Orange in neonates.	As in <i>L. melanocephala</i> or <i>L. stenophrys</i> .

Table 3. (cont'd)

1. Pough et al. (1978) note that black pigmentation on the head dorsum in viperid snakes may protect stored venom in the glands from detoxification due to exposure to UV light. Greene (1997) notes that rattlesnakes inhabiting high elevations (where UV would be increased) often have a higher melanin content than lowland conspecifics. Bushmasters, despite the presence of an eyestripe, scored low in melanin in the Pough et al. (1978) study. However, it is unlikely that Pough et al. (1978) were aware of the tremendous color variation in bushmaster species (they do not list sample locality), some of which have virtually no head pigment, and others, such as *L. melanocephala*, western Amazon *L. muta*, and the bushmasters of eastern Panama–northwestern Colombia, are highly pigmented dorsally. Dorsal head pigmentation in bushmasters may be associated with high elevations, overall reduced rainfall, and cooler habitats. Low temperatures require increased solar exposure by the snake; low rainfall suggests increased incidence of solar exposure, and high elevation indicates higher UV.

Hence, bushmasters inhabiting elevations greater than 1000 m such as *L. melanocephala*, or from areas of reduced rainfall, such as the eastern Panamanian forms, might benefit from a darkly pigmented head dorsum during basking in order to thermoregulate, as might bushmasters subject to more frequent solar exposure from other causes (e.g., those inhabiting tropical moist–dry transition forests). In my study, lowland *L. stenophrys*, with low elevation score and very high rainfall score, scored low in melanin, probably because of limited basking potential and low need to bask in consistently warmer climate. *L. stenophrys* collected from 1000 m in Cerro Azul, Panama, where temperatures are cool, had a higher than normal head pigmentation score for that species, while *L. stenophrys* from nearby lowland Chagres River scored much lower. Bushmasters from northeastern South America (Surinam) scored very low, for here the climate is hot, the rainfall high, and the elevations typically low. Some live specimens in captivity here possessed no black pigment anywhere on their bodies, and even the eyestripe was merely a reddish brown. Bushmasters from southern South America, such as *L. muta rhombeata*, which inhabit relatively high elevations and know a relatively cooler “winter” season, scored high, as did Mata Grosso *L. muta* of the same parallel. *L. muta* from the eastern Andean versants had much higher black head pigmentation than those from the Guiana Shield, in some cases (e.g., specimens from Pastaza, Ecuador) nearly full black. Ripa (1994) describes head basking in *L. melanocephala*, with the snakes keeping the main body concealed underground. Conceding head markings to be an adaptive trait, clinal increase in head markings may reflect historical proximity to cool mountain ecologies.

2. In deceased examples the tongue may turn black due to post mortem autolysis. No living bushmaster has a black tongue; hence Campbell and Lamar’s (1989) admirable general description for *Lachesis*, “The tongue [of *Lachesis muta*] is black,” is in error. These examiners were probably misled by preserved specimens. A valid point for interpolating live samples in morphological studies.

Table 4. Behavior and predation variation among bushmasters. Sources: Ripa (1994) and Ripa (unpubl. data).

Characters	<i>Lachesis muta</i>	<i>Lachesis stenophrys</i>	<i>Lachesis melanocephala</i>
Defense	May stand ground or flee the intruder. If provoked may strike from a fixed coil, but usually will not advance to attack. Gliding lunge toward the intruder is usually a closed-mouth bluff with no attempt to bite, merely to escape. Nervous temperament; however, makes <i>L. muta</i> unpredictable. Usually calm when encountered during the daylight, as if relying on camouflage for concealment.	Stands ground, seldom flees. If provoked, will strike from a fixed coil; if abruptly startled (usually in response to heat) may advance to attack, striking repeatedly. Strike may exceed 40% snake body length. Calm disposition typically; it is not easily provoked, and can often be approached closely and even picked up by the midbody without evoking strike-reactions.	Stands ground or may advance towards intruder from a series of looped, shifting coils (usually females); males sometimes flee. Nervous, irritable. The boldest, most dangerous and unpredictable of the bushmasters. During breeding season (after becoming impregnated) the female may pursue and chase intruders within range of her nest site. For accounts see Ripa (1994).
Predation frequency in captivity, snakes aged 2–6 yrs¹	4–6, 200–250 g rodents (<i>Rattus norvegicus</i>) monthly, except during reproductive period.	4–6, 250–350 g rodents monthly, except during reproductive period.	As in <i>L. stenophrys</i> .
Prey Size¹	Reduced. Max. size 300–400 g rodent; typically less than 300 g.	Increased. Max. size 350–525 g rodent, typically less than 400 g.	As in <i>L. stenophrys</i> .
Use of strike-hold to capture prey scored against strike-release (failure to maintain strike-hold)²	50% of the time strike-hold was accomplished with 250 g rodents.	70% of the time strike-hold was accomplished with 250 g rodents.	As in <i>L. stenophrys</i> .
Strike-hold prey size capacity²	Max. of 350 g; typically not more than 250 g.	Max. of 400 g; typically not more than 350 g.	As in <i>L. stenophrys</i> .
Prey recovery and ingestion after strike-release of prey in an area 15 m square³	If prey escapes to within 1 m from snake’s head, rate of recovery and swallowing approaches 80%. Beyond 2.5–3 m, rate is less than 14%.	If prey escapes to within 1 m from snake’s head, rate of recovery and swallowing approaches 70%. Beyond 2.5–3 m, rate may be less than 10%.	As in <i>L. stenophrys</i> .
Arboreality⁴	Increased.	Reduced.	Reduced.
Activity⁵	High.	High.	High.

Table 4. (cont'd)

Characters	<i>Lachesis muta</i>	<i>Lachesis stenophrys</i>	<i>Lachesis melanocephala</i>
Adaptation to Captivity ⁶	Difficult, nervous.	Not difficult. Calm; adapts readily under appropriate conditions.	Very difficult. Nervous, excitable.

1. See section in text on “Prey size and predation frequency.”
2. Based on observations of live prey offered in normal feeding regimes. This involved bushmasters of all ages and sizes, ranging from neonates to very large adults up to 10 years old and 10 kg. See section in text on “Strike-hold Behavior.”
3. One of the frustrations of offering live prey to bushmasters in large room areas is the amount of wastage of prey items. If the prey is strike-held, and within the right size limits, it will almost always be eaten. But if the prey escapes the strike-hold maneuver of the snake, the chances of it being successfully trailed are much reduced. If the prey escapes to more than 2.5–3 meters from the snake, it will probably not be trailed and eaten. There is no doubt the snake *could* trail the bitten animal (one must assume the bushmaster to be as competent at chemosensory maneuvers as a rattlesnake) but the hunt-strategy of the bushmaster seems to be not to do so, rather to remain near the hunting site and, one must assume, await another chance at a kill.
This hesitance to trail prey may relate to the amount of time it takes strike-released rodents to die, which may not always be rapid and commonly exceeds 1–3 minutes even when strike held, and up to 10 minutes or longer when strike-released (I have recorded it taking as long as several hours; compare to the more rodent-toxic *Bothrops*, Table 8, where the prey dies within seconds). “Successful Prey Recovery” gives an idea of the dependency of these snakes on strike-hold. These figures result from 100 sequences (with each species) taken from normal working conditions in the maintenance of these snakes, scored against number of dead (or envenomated but still living) prey animals that have been recovered at various distances from the strike-releasing snake, which did not trail and eat them. These sequences do not represent “ambivalence to feed” since the snakes could be observed visibly *attempting* to trail the bitten prey within a 1 m radius, and then giving up and returning to the ambush-coil. Moreover, when the dead (and now cold) prey was recovered, and heated to approx. normal live-body temperature, a second strike-hold sequence could be induced when reintroducing the prey item to the snake. If the prey was then strike-held, or struck and then left within the snake’s near radius, normal feeding operations followed. But if a second strike-hold could not be induced, the prey was usually not consumed. Hypothesis: reluctance to trail prey that is not strike-held and escapes, may result from (1) prey exceeded size threshold; (2) low probability of recovering lost prey, which, in the frequently inundated forest floor could be difficult to trail; and (3) length of time for a bitten rodent to die increasing its chance of escaping to a distance where it could not be recovered by chemo-trailing. Amending Greene and Santana’s (1983) conclusion (which reads: “The hunting strategy of the bushmaster appears to be, find a ‘good’ place to ambush prey, feed infrequently on large items, and minimize detection by enemies.”), I offer the following new hypothesis: The predatory strategy of the adult bushmaster appears to be: *find a good place to ambush prey, feed frequently on small prey that can be strike-held, and avoid use of chemosensory trailing beyond a specific near distance*. Chemo-trailing escaped prey requires temporarily “losing” a proven-successful ambush-site in favor of a precarious and possibly unsuccessful search for prey that may have escaped to distances outside the snake’s capacity to recover it (an alternative hypothesis: chemo-trailing prey for great distances might entail losing the chemical trail to the home-burrow, also easily lost in the rainy forest environment; see text). Unsuccessful prey trailing wastes hunting time, and in the perpetually rainy conditions of the forest, good hunting time can be at a premium. If prey escapes strike-hold, hunting time may be more effectively managed by trying to ambush another prey item than in searching for dying prey. Small prey is preferred because it is always easiest to strike-hold and thus prevent from escaping, but it is also easier to digest at the reduced temperatures of the high elevations and continuously rainy diurnal shade habitats of these snakes. Very large prey (above 450–500 g) swallowed by bushmasters usually results in regurgitation at reduced temperatures such as is typical in mountain rainforests (20–23°C) (see below).
4. “Arboreality” is based on captive observations recording frequency of bushmasters to climb above heights of 1.5 m in an enclosure space of 4.2 × 3.6 × 2.4 m high. *Lachesis muta* scored the highest as a climber, with 3.1 hours to every 2.2 hours for *L. melanocephala*, and 1.4 hours for *L. stenophrys*.
5. “Activity” is based on captive observations of movements in large enclosures (4.2 × 3.6 × 2.4 m high; for a more complete description of the enclosure, see Ripa [1994]). Bushmasters scored very high when compared with *Bothrops*, being relatively more active by an unexpected 4.3 hrs of activity (for bushmasters) to 1.4 hr of activity for *Bothrops asper*, *B. atrox*, and *B. leucurus*, averaged over a 12-month period. “Activity” was defined as (1) relocation to a coil more than 40 cm away (for bushmasters), and 20 cm away for the smaller *Bothrops*; (2) crawling to “explore”; (3) crawling to hunt; (4) crawling to engage in male combat; (5) crawling to court and breed. Surprisingly, the quick-moving *Bothrops* group proved by far to be more inactive than the slow-moving but frequently crawling bushmasters, regardless of the size or amount of food they consumed (note: *Bothrops* do not male combat, and breeding, typically reciprocated early-on by females, does not require much ritual activity of males, unlike with bushmasters). While this does not prove conclusively that bushmasters are “more active” than *Bothrops*, it challenges the popular notion of the “sluggish, cryptic” bushmaster as it is frequently portrayed in the literature (e.g., Greene and Santana [1983]). Among venomous snakes, only the elapids scored higher than the bushmasters for activity. The active life habits of bushmasters are inextricably linked to prey size, which, as I have shown, is relatively small for a snake of its size, and *requires the snake to feed frequently*. (Note: activity in snakes is always temperature related. I used temperatures ranging from 24–27°C, these temperatures being reduced during breeding season to 20–23°C for short periods to induce courtship and male combat). See section in text on “Activity and concealment.”
6. Based on adult specimens captured from the wild and acclimated to captivity.

Table 5. Distribution and habitat for three species of bushmaster, and one probable new species.

Characters	<i>Lachesis muta</i>	<i>Lachesis stenophrys</i>	<i>Lachesis melanocephala</i>	Darien bushmaster
Countries where found	Brazil; French Guiana, Surinam, Guyana, Venezuela, Trinidad, southern Colombia, eastern Ecuador, eastern Peru, northeastern Bolivia. ¹	Southern Nicaragua, Atlantic Costa Rica, and Atlantic and Pacific Panama (Canal Zone region), northwest of Chepo region, Panama province. ²	Southeastern Costa Rica, especially vicinity of Peninsula de Osa. ³	Southeastern Panama, east of the dry forests of Chepo region, Atlantic and Pacific Colombia. Pacific Ecuador, and the inter-Andean valleys of Colombia. ²
Ecogeography and rainfall	Tropical wet and moist forests. ⁴ Rainfall intermediate to high, 2500–6000 mm. ⁵	Tropical wet and moist forests. ⁴ Rainfall very high, predominately 3500–6000 mm range. ⁶	Tropical wet and moist forests. ⁴ Rainfall relatively low 2500–4000 mm. ⁶	Tropical wet and moist forests ⁴ and tropical moist-dry transition forests. ⁷ In eastern Panama cloud forest occurs on ridges as low as 750 m, ⁸ making these snakes also probable inhabitants of cloud forest. Rainfall lowest of the bushmasters, predominately 2000–2500 mm range, but may reach 4000 mm at high altitudes. ⁹
Elevation preferences¹⁰	100–700 m. Most often encountered above 200 m.	100–700 m. Most often encountered at 200–400 m.	300–1000 m. Most often encountered at 300–800 m.	Probably similar to <i>L. melanocephala</i> .
Elevation Limits	Up to 1000+ m. ⁵	Up to 1000 m. ³	Up to 1500 m. ³	Probably similar to <i>L. melanocephala</i> ; an example was collected at 820 m; another specimen came from Cerro Cituro, Darien, Panama, at 1100 m. ²
Population Density	Uncommon. Dispersed. 200 person-hours. ^{11, 12}	Not uncommon in some median elevations 75 person-hours. ¹²	Rare in lowlands, most often found at high elevations 400 person-hours. ¹²	Insufficient data.
Habitat preferences and limits	Diurnal shade, favors high shields, mountain versants, avoids lowlands, swamps and coastlines. ²	Diurnal shade, mountain versants, avoids lowlands, swamps; has been taken from near sea level in suitably humid forests, however, avoids coastlines. ²	Diurnal shade, mountain versants, avoids lowlands, swamps, rainshadow, coastlines, seldom found at sea-level. ²	Probably not dissimilar to other species; however, would appear to have greater tolerance for dry climate, especially in eastern Panama.

1. Hoge (1965); Taylor et al. (1974); Hoge and Romano-Hoge (1981).

2. Ripa (unpubl. data) and Ripa (in prep.). The Caribbean coast dwelling *L. stenophrys* inhabits a rainier climate than the bushmaster of eastern Panama (two to three times the rainfall of the latter [Ministerio de Obras Publicas Panama, 1993]), at lower elevations and with lower exposure to UV light. The Darien bushmaster inhabits a significantly drier ecology than perhaps any other member of the genus, in regions given to high elevations (along the northwestern Andean versants), and greater exposure to UV light in the less shaded transitional forests. Despite this, it is even found in cloud forest, which in eastern Panama (unlike other parts of Central America) can exist at elevations as low as 750 m (Myers, 1969). The evolutionary shaping of the bushmasters might not depend entirely on vicariance. An animal exists because it is better adapted to some ecological niche than its competitors. The wet-climate inhabiting *L. stenophrys* might have failed to penetrate the drier habitat of the Darien snake simply because it could not survive there, the loser in the game of intraspecific competition. Habitat differences that might not limit a highly opportunistic and adaptable species like *Bothrops asper* might have greater impact upon the highly specialized primary rainforest dependent bushmaster.

3. Solórzano and Cerdas (1986).

4. Vial and Jimenez-Porras (1967).

5. Campbell and Lamar (1989).

6. Tosi (1969, 1971).

7. Ministerio de Obras Publicas Panama (1993).

8. Myers (1969).

9. Myers et al. (1978).

10. Refers to those elevations where the author has had the most success finding these species. Ripa (unpubl. data, 1979–1998).

Table 5. (cont'd)

11. Duellman and Salas (1991).

12. Refers to the average number of person hours it takes to find a bushmaster. Obviously this has no factual basis, being a sampling of personal experiences looking for bushmasters, averaged from hours spent searching for them divided by numbers of finds. Based on long experience, however, the writer considers these numbers a good rule of thumb.

Table 6. Reproductive behavior, reproductive biology and related data for three species of bushmasters. All sources Ripa (1994) and Ripa (unpubl. data) unless otherwise noted. All data having a source in "Ripa" based on reproductions of wild caught adults acclimated to captivity; and of second generation unrelated sexual pairs.

Characters	<i>Lachesis muta</i>	<i>Lachesis stenophrys</i>	<i>Lachesis melanocephala</i>
Sexual maturity	Probably as with other species.	At 13–14 months males have been noted trying to court females. Females can reproduce at age 2.5 years.	As in <i>L. stenophrys</i> .
Typical breeding season¹	March–May. However, probably variable in this wide-ranging species.	February–April.	January–April.
Use of "ridge-sawing" to stimulate female²	Never observed.	11 instances out of 19.	10 instances out of 22.
Male combat with duration³	Mild. 4 hours.	Violent. 6 hours. As in <i>L. melanocephala</i> .	7 hours. Violent spiraling with complete inversion of entwined bodies. Dominated male usually flees. This ritual does not involve "ridge-sawing."
Necessity of male combat to stimulate breeding	None noted.	None noted.	None noted.
Necessity of presence of females to stimulate male combat	None noted.	None noted.	None noted.
Temperature reduction to stimulate breeding	Probably 23.9°C. ⁴	20–21 + °C. Maintained for 2 weeks.	20–21 + °C. Maintained for 2 weeks.
Typical ambient temperature at time of breeding	25–27°C. Uncertain because copulation was not observed. ⁴	25°C during observed copulation.	22°C, 25°C during observed copulation.
Ambient humidity at time of breeding	70% ⁴	70–95%	70–95%, however, has occurred in several instances as low as 50%, with little prior temperature manipulation.
Barometric pressure reduction to stimulate breeding⁵	Unknown, probably similar to other species.	Not necessary; snakes will breed regardless.	As in <i>L. stenophrys</i> .
Aggressiveness of males during breeding season	No increase noted.	No increase noted.	No increase noted; however, males will become bolder towards intruders, although not necessarily with intent to attack them.
Aggressiveness of females during pregnancy	Very few observations.	Noted; may become aggressive during pregnancy and defending the potential nest site.	Noted; may become <i>highly</i> aggressive during pregnancy and defending the potential nest site. See Ripa (1994).
Orientation method of sexual pairs	Not studied; probably as for others.	Female crawls a specific radius leaving chemical clues; males may leave sperm deposits. See Ripa (1994).	As in <i>stenophrys</i> .
Site of copulation	Probably as with other species.	Open area, not within burrows.	As in <i>stenophrys</i> .

Table 6. (cont'd)

Characters	<i>Lachesis muta</i>	<i>Lachesis stenophrys</i>	<i>Lachesis melanocephala</i>
Duration of copulation	Probably as with other species.	Usually nocturnal. 5–7 hrs, at intervals of 5–10 days during the breeding season.	As in <i>stenophrys</i> .
Duration of pregnancy	No data.	101 days typically, but has lasted as long as 130 days. A short pregnancy of 93 days has been observed in a single instance.	As in <i>stenophrys</i> .
Feeding of females during pregnancy	Probably as with other species.	Continuous in some specimens; others infrequently; many will not feed at all.	As in <i>stenophrys</i> .
Site of oviposition	Ripa (1994) reports removing a female with 19 eggs from an <i>Agouti paca</i> burrow.	Concealed within a burrow in near darkness.	Concealed within a burrow in near darkness.
Number of eggs	Typically 9–13; may reach 19, as in above instance.	Typically 9–13; up to 16 recorded.	As in <i>L. stenophrys</i> .
Mean egg dimensions at time of oviposition (mm)	41.8 × 75.9 ⁴	56 × 64 40 × 55 48 × 61	55 × 72 50 × 90
Mean egg weight at time of oviposition (g)	82.2; however, only one of 10 eggs was weighed. ⁴	91	80 110
Thermoregulation of eggs	Ambient.	Ambient. Bushmasters do not thermogenically shiver.	Ambient.
Laboratory incubation temperature	30–31°C. ⁴	26–28°C ⁶ , 24°C, 28°C, 30°C.	24°C, 28°C, 30°C. I have noted higher hatch rate with median temperatures, but this may be coincidental.
Duration of incubation	61 days. ⁴ Up to 79 days at reduced temperatures.	60–79 days; 77–90 days. ⁶ Ave. 75–77 days at 24°C. Ave. 61 days at 30°C.	60–79 days, may reach 90 days at reduced temperatures. Ave. 75–77 days at 24°C. Ave. 61 days at 30°C.
Hydroregulation of eggs ⁷	See remarks.	See remarks.	See remarks.
Duration of egg guarding by female	Probably until hatching.	Until hatching.	Until hatching; however an example has been observed to abandon her oviposition site five days prior to hatching of her young, which occurred in another enclosure.
Feeding of female during egg-guarding	Does not feed.	Does not feed.	Does not feed.
Drinking of female during egg-guarding	Probably limited, has not been observed.	Probably limited, has not been observed.	Probably limited. In a single instance the mother snake has been observed to leave her nest to drink from a water bowl (she then returned to guard the egg site as before). In the wild the mother snake probably need only protrude her head from the burrow in order to drink from available rainfall.

Table 6. (cont'd)

Characters	<i>Lachesis muta</i>	<i>Lachesis stenophrys</i>	<i>Lachesis melanocephala</i>
Orientation of female to oviposition site	Not studied.	Chemosensory.	Chemosensory.
Aggressiveness of female during egg guarding	Above normal.	Above normal; hissing, gular inflation, tail vibration, but will not leave the eggs to attack.	Above normal; hissing, gular inflation, tail vibration, but will not leave the eggs to attack. Females guarding the nest site are most dangerous <i>before</i> the eggs have been laid, not after.
Neonate mean total length (mm)	463 ⁴	406	533
Neonate mean weight (g)	50 ⁴	45	75
Aggressiveness of neonates and juveniles	Higher than adults.	Higher than adults.	Higher than adults.
Sexual dimorphism	Males larger than females; broader tail base may not be apparent to the eye; have noted no increased percentage of males with dark vertebral stripe.	Males larger than females; have visibly broader, longer tails with more subcaudals; percentage of males with dark vertebral stripe higher than for females.	As in <i>L. stenophrys</i> . In adults, males retain vestiges of light color line separating the black head cap from the postocular stripe; males may have a speckled ground color where in females the ground color is typically more clear.

1. In *L. muta*, extrapolated from oviposition dates of wild caught females that have laid eggs in captivity, compared to observed length of pregnancy in other species. In *L. stenophrys* and *L. melanocephala*, from repeated observations in captivity over a five-year period.
2. Based on observed rituals ending in copulation. First described in Ripa (1994), ridge-sawing (RS) behavior involves the male inverting his body onto the dorsum of the coiled female. Using his pronounced dorsal ridge he begins a vigorous “sawing” of the rasp-like dorsal scales against the rasp-like dorsum of the female. The exact purpose of this strange and unparalleled ritual among snakes—whether it is to sexually stimulate the female, or merely to irritate her into uncoiling so that he can align her—is not certain. It occurs most frequently when the female is resistant to the courtship advances of the male snake; however, if the female presents herself willing to the male—here cloacal gaping of the female (sensu Armstrong and Murphy [1979]) is usually observed—typical crotaline body alignment will occur and the RS ritual may be obviated. Since Ripa (1994) appeared, this ritual has also been observed in a courting pair of *L. stenophrys* at Gladys Porter Zoo (pers. com., C. Hairston Adams, Curator of Reptiles, Gladys Porter Zoo).
Courtship in bushmasters is probably more violent than in any other crotaline snake (Ripa 1994); however, RS behavior is never used in the even more violent male combat dance. But while an important aspect of courtship, RS behavior alone would not be a compelling reason for the origination of the prominent middorsal ridge (see Table 8). Rather the application of the ridge in the sexual language may be important in seeing that this trait is successfully passed on to future generations. Viewed from the standpoint of natural selection, the male bushmaster “without” such a ridge and with much diminished ridge scalation might find himself unable to copulate with the resistant female (why resist males at all except as a selective process?)
3. Based on 20 observed combat rituals. Ripa (1994) did not report significant male combat in Central American bushmasters, nor has it been documented among South American *L. muta*. Further observation, however, reveals male combat in both species of Central American bushmasters to be as advanced—and spectacular—as that of any other crotalid. Two, three, or even four male bushmasters, each exceeding 2 m and 7 kg, locked together, fighting to attain a dominant position, and turning 360-degree somersaults in the air while employing violent thrusting motions of their coils, are sufficient to demolish the naturalistic interiors of the snakes’ enclosures, and threaten to break the glass out of the cage. Typically male combat begins after dark but has been seen in the daylight hours as well; light does not much seem to impede it. Seasonally, it may occur daily for up to 9–10 days; cease for a week, two weeks, a month or more, only to resume again sequentially as before. A sudden drop of temperature, or maintaining cooler than normal temperatures for long periods (usually below 22°C), has been observed to trigger it. No greater incidence of copulation with females has occurred because of male combat. If anything, less reproductive activity has occurred in cages that possessed multiple males, as males would seemingly prefer to combat than court females if other males are available. Once the combat response is triggered in these snakes, it is not easily “turned off” except by removing the spare male or males. I suspect the persistent presence of males (one of which, in the wild, would normally flee the scene) actually impedes breeding of these snakes in captivity. Perhaps if other males remain present, combating hasn’t been successfully finalized. In response to this I have begun to remove any additional males after the first combat sequence of the breeding year.
4. Boyer et al. (1989).
5. Higher breeding incidence associated with decreased atmospheric pressure is probably related to greater general activity of these (and most snakes) during storm activity, but not to actual increased reproductive interest. Decreased atmospheric pressure (which significantly also usually accompanies a loss of temperature) may be incidental to breeding, but does not necessarily trigger it. The pairs merely encounter each other more often because of greater exploratory crawling. It is noteworthy that bushmasters will not breed while being “rained on” but require a “dry period” in which to court and copulate. Thus the idea of a frontal condition with an accompanying rainstorm prompting breeding behavior is to some extent contradictory. The snakes would probably not breed until well after the storm was over, not during.
6. Solórzano-Lopez et al. (1987).
7. Somma and Fawcett (1989) have shown hydric changes to be a consequence of the presence of the nesting female prairie skink (*Eumeces septentrionalis*) with her eggs. In the case of the bushmaster, the very large, atmosphere displacing, respiring and uric-acid excreting mother snake, coiled tightly about her eggs in an enclosed nest site (the burrow) would make some form of hydric changes inevitable. However, to what extent, if any, her presence as a “hydroregulator” may improve the success of hatching has not been studied.

Table 7. Growth in toal length and weight for three species of bushmasters. All sources Ripa (1994) and Ripa (unpubl. data). For a comparison with *L. muta* neonates through age 16 months, see Boyer et al. (1989).

Age	<i>Lachesis muta</i>	<i>Lachesis stenophrys</i>	<i>Lachesis melanocephala</i>
Hatchling	489–542 mm 50 g	401–436 mm 45 g	510–548 mm 75 g
6–7 months	731–1100 mm 340–480 g	710–1070 mm 450–600 g	871–1180 mm 675–750 g
20 months	1497 mm 1620 g	1224 mm 2553 g	1534 mm 2500 g
3 years	1900 mm 3500 g	1650–1800 mm 4000–5000 g	1940 mm 5000 g
4 years	2240 mm 4000–4200 g	1800–2000 mm 5000–6000 g	2000–2200 mm 5000–7000 g
5 years	2500+ mm 5000 g	2200–2230 mm 7000–8000 g	2200–2400 mm 7000–8000 g

Above examples are sizes of bushmasters at various ages in captivity. After four years, growth in length appears to stabilize to within a few centimeters per year, although growth in mass may increase somewhat more substantially. Trends may be noted: greater elongation of *L. muta*, but lower overall body weight compared to the stockier but less elongate *L. stenophrys*.

Growth of bushmasters is dependent on food intake. These three species were fed according to a nearly identical regime of weekly and biweekly feedings, graduating in prey size to meet their growing food capacity. However, it should be noted that the prey-size threshold, being lower for the more slender *L. muta*, resulted in a lower overall consumption of prey weight by *L. muta*, although the numbers of prey items consumed were similar. The increased bulk and weight of Central American examples vs. the greater slenderness, but actually greater elongation, achieved by *L. muta* suggests that *L. muta* is able to grow longer (although not larger), with less food.

Hypothetically, captive-raised snakes should grow faster than wild snakes, owing to supposed increased availability of food in captivity (and presumed inconsistency of available food in the wild) and lack of parasites in the snake. However, this tacitly accepted idea might not always be true in actuality. The really large bushmasters that have been seen have all been taken from the wild; and thus far no captive-reared example has approached the size of the 11.7 ft giant described by Ditmars (1910). In captive collections in America, the longest—but not the largest—living bushmaster of which I have a record was collected by native persons for Theo Henzen, in Surinam (T. Henzen, pers. com), and later owned by Paul Bartlett, of San Antonio, Texas (Paul Bartlett, pers. com.). This wild-caught *L. muta* was verifiably 3400 mm at time of capture. In captivity, most growth in bushmasters takes place in their first six years: hence, the idea that the very large bushmasters such as were seen by Ditmars would have to be very old snakes is probably not factual. Ditmars’ big bushmaster may have been old, but it didn’t *have* to be. In all likelihood its near full length was achieved within its first eight years of life. After this time, growth rate is so minimal that 10 years might be required for a snake to gain even as much as 30 cm.

Ripa (1994) reports *L. muta* being the longest (but not the largest) of the bushmasters, based on Hoge and Lancini (1962) and corroborative information gathered at wildlife dealers in Surinam. In South America, bushmasters of the size collected by Henzen are not so very unusual; while in Central America such elongate examples are very scarce. I have never measured a wild caught Central American example in excess of 2.7 meters, nor can I find an authentic record of one in the modern day. Ditmars’ 11-foot, 7-inch, giant *L. stenophrys*, probably measured prior to 1910, remains the largest bushmaster on record. Hoge and Lancini’s (1962) reference to specimens of *L. muta* reaching 4.5 m cannot be substantiated with a specimen.

Given the observed growth rate of bushmasters, it is not impossible that such large examples could exist in the modern day. However, size makes a snake a better target, and the sheer conspicuousness of such large examples in areas frequented by hunters and agricultural workers would only make them easier to exterminate. Consequently, Central America, which has no remote wildernesses of the scale to be seen in South America, probably cannot support snakes of the great size it did in the past.

Concealment for large snakes is more difficult to find and the choice of underground burrows becomes more limited when the snake surpasses a certain size threshold. In peccary (fam. Tayassuidae) country, effective concealment can be an urgent matter for a ground-dwelling snake. These “wild pigs” travel in herds of up to 100 individuals (Nowak, 1991). They can both devour a bushmaster and survive its bites, according to local testimonials. The rarity of finding serpents of any kind in primary forest in the Neotropics is probably directly related to the occasionally ophiophagous appetites of peccary forcing snakes to seek out secure underground burrows in order to avoid detection.

Table 8. Adaptation comparisons between sympatric Neotropical terrestrial viperids—the bushmasters (*Lachesis stenophrys* and *L. melanocephala*) and the terciopelo (*Bothrops asper*): “*A competitive game.*” All sources Ripa (1994) and Ripa (unpubl. data) unless otherwise noted.

Characters	Bushmaster (<i>Lachesis</i> sp.)	Terciopelo (<i>Bothrops asper</i>)
Range of prey size	Small. Relatively inelastic jaws, and narrow neck and throat make this snake a uniquely inefficient prey swallower. Proportionate to its size, the prey-size threshold for the bushmaster is perhaps the smallest of any large snake: a rodent of 500–600 g being the largest observed successfully engulfed, and this by an enormous <i>L. stenophrys</i> of 2.5 m (weight 10 kg). Feeds on mammals and birds exclusively, within a certain size threshold.	Large. Jaws very elastic, throat extremely distendable. A <i>B. asper</i> weighing less than 2 kg, with its proportionately very large head, can engulf prey comparable to a bushmaster of 2.5 m and 10 kg. Large females can consume prey in excess of 1000 g, or about twice the prey size threshold of the largest bushmaster. Greene and Hardy (1989) describe adult females weighing 1.1–2.2 kg taking prey the size of opossums (<i>Didelphis marsupialis</i>) and rabbits (<i>Sylvilagus brasiliensis</i>). Feeds on a wide variety mammals and birds; young specimens will eat reptiles and amphibians.

Table 8. (cont'd)

Characters	Bushmaster (<i>Lachesis</i> sp.)	Terciopelo (<i>Bothrops asper</i>)
Frequency of feeding	Frequent. Small prey size necessitates frequent feeding for these snakes in order to attain characteristically large size. Bushmasters will leave their hide-sites to hunt almost nightly, taking ambush-hunting stance coils at specific sites where accustomed to capturing prey. Sexually mature males may cease feeding (or feed sporadically) during the 1–3 month breeding season. Females, during the reproductive season, and once impregnated, may begin a three to six months fast. Although some will continue to feed while gravid, none have been observed to feed while egg-guarding. During the six months prior to the breeding season (after completing egg-guarding), females will consume enormous numbers of rodents—often exceeding their own body weight in total amount.	Frequent. However, capacity to engulf large prey enables these snakes to remain relatively inactive for great periods of time, sufficing on a single large meal. Females continue feeding during gestation, although infrequently; males also feed very little and some will fast during the entirety of the breeding season.
Strike-hold versus strike-release	Strike-holds prey almost exclusively. Strike-release is employed only by “default” (i.e., the snake fails to maintain strike-hold) and not used facultatively as an alternate hunting strategy.	Adults use strike-release; neonates use strike-hold and facultative strike-release. An ontogenetic shift toward greater strike-release occurs after the snake reaches about 6–8 months age. Adults, however, will employ strike-hold when feeding on small prey (e.g., mice as opposed to adult rats).
Speed of prey digestion	Intermediate to most vipers. Average 14 days between excretions, with digested prey excreted in a single defecation. Seldom if ever basks in sunlight in order to aid digestion; rather it takes concealment during this period, usually underground.	Rapid, relatively large prey may be digested and excreted in as little as 5–7 days, usually in multiple defecations. Digestion may be aided by basking in sunlight.
Body build	Heavy, muscularly taut, laterally compressed, with an almost armored exterior conformation—capable of short bursts of speed, but not to the extent of <i>B. asper</i> . These snakes possess a pronounced middorsal ridge with a heavy spinal column, and a strong lateral body compression. Hypothesis: the ridge and body compression, which is most developed anteriorly, braces the reptile’s neck and spinal column against the struggles of live prey when seized and held elevated in the strike-hold maneuver. This special adaptation serves as an “overhead truss system” to better manage the weight of the prey. When, in another strategy, violently struggling prey is pressed vertically against the ground surface, the reinforced spinal column with its high neural spines anchored in the fleshy ridge acts as a brace against deflection. This vertebral conformation is shared by <i>Atropoides nummifer</i> , a squat viperid with a pyramidally conformed body cylinder, inhabiting somewhat higher elevations than bushmasters in Central America. <i>Atropoides nummifer</i> is significantly also a strike-holder of prey (Chiszar and Radcliffe, 1989). The whole physical aspect of the bushmaster, with its ridge-dorsum, thick vertebral column, lateral body compression, and relatively very heavy musculature for a viper, would seem evolved toward a physical potential for strike-holding resistant prey, and keeping it elevated while seized in the jaws for long periods of time—up to 10 min has been observed before prey was repositioned for swallowing.	Slender, flexible, with round body conformation, and no comparable vertebral ridge—built for speed. Large adults may reach considerable girth, however, with a body weight in excess of 6 kg.
Head size	Small proportionate to body length. However, the head is box-like and thick, probably to deflect against prey struggling in strike-hold position and to house the enormous fangs (which may be visible through the skin in the distension of the gular area). Snakes that must <i>hold on</i> to their prey often evolve pronounced dentition: <i>Bitis</i> , <i>Bothriechis</i> , <i>Corallus</i> , <i>Morelia</i> , etc.	Large proportionate to body girth and length. Relative to body mass, females of this species have perhaps the largest head of any terrestrial viper. However, compared to the box-like head conformation of the bushmasters, the head is relatively flat for its great length and width. Strike-release strategy may make an evolved vertical head conformation unnecessary.

Table 8. (cont'd)

Characters	Bushmaster (<i>Lachesis</i> sp.)	Terciopelo (<i>Bothrops asper</i>)
Scalation	Rugose, with heavily beaded, rasp-like scales. Scale conformation may be tied to microhabitat of underground animal burrows. The bushmaster makes use of these scales and the pronounced dorsal ridge to excavate passages for itself underground. In captivity, Central American bushmasters burrow in mulch or soil substrate with the head and rasp-like neck used to excavate (a depth of 30 cm has been recorded creating a tunnel approx. 10 cm wide). Bushmasters invert their bodies and perform sawing movements in mulch substrates to excavate places in which to coil.	Much less rugose, with conventionally keeled scales. Have observed no instances of burrowing, or body sawing.
Loreal folds	Conspicuous. In strike-hold maneuvers the large lip-shields, from a loreal fold, slide over and protect the eyes and heat pits from the retaliation of the rodent prey. ¹	Adults strike-hold only relatively small prey that is easily overpowered and does not constitute much of a threat to the snake. Perhaps the large lip shields play some role in protecting the eyes and heat pits in the quick strike, but this would seem not to be a very evolved characteristic. There is no evidence of its usage in neonate strike-hold episodes—the eyes and heat pits remain exposed when the prey is seized.
Microhabitat	Moist (necessary for hydoregulation of the snake's skin and its eggs during incubation). Terrain hilly and elevated (prevents water standing in burrows where eggs are guarded). Not adaptable to swamps, avoids pasture, agriculture (except cacao and bush-planted banana), rare in secondary forest. Cannot tolerate much heat or dryness. Not very adaptable	Moist, hot, dry. Adaptable to most any tropical environment or agricultural situation, but will usually avoid tropical dry forest. ¹
Elevation	To 1,500 m (<i>L. melanocephala</i>), ² but usually below 1,000 m. ³	To 2,600 m. ²
Use of basking for thermoregulation	Low. Skin is easily dehydrated by heat, causing dysecdysis. This snake has a strong preference for diurnal shade and usually avoids intense sunlight, although will bask for short periods in cooler morning hours in the wild. Ripa (1994) records head-basking in <i>L. melanocephala</i> , but observations of full-body basking in captivity are rare outside of gravid females, an example of which has been seen at Dallas Zoo (Boyer et al., 1989).	High. Frequent basking enables these snakes to inhabit higher elevations than bushmasters, and enables them to digest relatively larger meals faster. This snake's skin is sun-tolerant, and dysecdysis is seldom a problem even with minimal moisture. Hence its great success in agricultural areas.
Reproduction	Egg-laying. 6–12 annually. Females may skip breeding one out of every 3–4 breeding years. Duration of pregnancy averages 101 days, with additional incubation period of 60–77 days. Hatchlings are large (up to 50 cm), well able to fend for themselves, and capable of taking large prey, such as an adult mouse. Perhaps these advantages offset low clutch size. Unlike <i>Bothrops</i> spp., however, young are limited to taking warm-blooded prey.	Live bearing. Annually. Duration of pregnancy is 180 - 240 days ¹ . Males and females capable of reproduction at 1.5 years age, or 1 m length (pers. obs.). Up to 100+ young, typically about 30–50. Most prolific viper in the Americas. ¹ Young are small compared to bushmasters, about 20 cm (pers. obs.), and would be easy prey to a variety of predators. However, they are omnivorous, can eat frogs, lizards, ¹ small mice, shrews, etc., and this may increase survival chances.
Concealment	Specialized requirements because of large size; large hollow logs, animal burrows, and may be reliant on these situations for guarding eggs. Relatively slender body conformation is perhaps a specific adaptation to life in narrow underground burrows—a large squat snake capable of reaching the body length of the bushmaster might be unable to conceal itself. Conspicuous in spite of good camouflage, this species is easily exterminated by man.	Smaller size and flexible body enable it to hide almost anywhere. Can flatten itself out beneath a log or a stone; can hide in trees or in low elevated brush, especially the “bowls” of dead palms. I have collected small specimens hiding under people's mattresses and within household furniture! There are reports of people being bitten in their beds! Impossible situations for a bushmaster of any age or size. Ease of concealment, superb camouflage, arboreality, prolificness and ease of adaptation make this species very resistant to extermination by man.

Table 8. (cont'd)

Characters	Bushmaster (<i>Lachesis</i> sp.)	Terciopelo (<i>Bothrops asper</i>)
Defense	Stands ground, or slow to escape; relies on camouflage. Will strike/bite usually only from the coil, and normally only in response to heat. Seems not to rely much on visual information to gauge a strike.	May coil to strike or rapidly flee, turning and striking as it goes; may strike from any body position, requires no fixed coil, and strikes in response to visual information as much as heat. These snakes are very fast and agile in escaping enemies, moving with racer-like speed.
Arboreality	Occasional, but decreasing with adulthood as snake's size increases. Higher for lighter-bodied South American forms than for Central American forms.	Lighter build makes this snake a good climber to almost any height in appropriate foliage; it is occasionally encountered in low trees, where, judging from stomach contents, it raids the nests of birds.
Venom effects on prey	Not very toxic to rodent prey. ⁴ Envenomated prey may survive for many minutes after the bite—long enough to put itself well out of range of the snake (pers. obs.). Prey not strike-held often escapes to distances outside the snake's capacity, or willingness, to trail it. In captivity this distance may be as little as 2–3 m. Bushmasters feed according to response-sequence integration triggered by strike-response to heat—chemosensory cues are needed only to induce prey-trailing and repositioning for swallowing, but a prey-response strike with strike-hold can often be triggered by <i>any warm object</i> even without chemocues from typical prey. ⁵ (For a type of “response-sequence integration” in rattlesnakes, see Chiszar et al. [1977]). Apparently, if the snake does not chemosensorily relocate the bitten rodent within a certain time frame it “forgets” to keep looking for it—which is to say, the response-sequence input triggered by the heat-strike wears off. Since in the frequently inundated environment of the forest chemical trails may be rapidly obliterated, the advantage of prey-trailing vs. loss of orientation to ambush-hunt site and/or site of proven-effective concealment (always limited for these large snakes) may be much diminished.	Very toxic to rodent prey. ⁴ Prey usually dies within seconds of the bite (pers. obs.). Will trail strike-released prey for distances as great as 10 m. Bitten rodents seldom make it that far. In an amazing number of instances the bitten/fleeing rodent becomes so disoriented as to return full circle and die within centimeters of the snake's head. Do some snake venoms “cause” dying prey to return to the bite-scene? It seems significant that bitten rodents seldom flee in a single direction <i>away</i> from the site of the snakebite, but spiral gradually back to the source of pain.
Bites on humans: occurrence	Rare. Humans and bushmasters seldom meet, owing to remote primary forest habitats of these snakes.	Frequent. Small size and adaptation to agriculture put these snakes into frequent contact with human beings. Probably most persons are bitten within a few hundred feet of their own homes, on their way to bathe or to the latrine
Bites on humans: mortality	High mortality. ⁶ “. . . easily inflicts the most lethal bite of any known pitviper . . . a fatality rate of 46% (5 of 11 cases (appears to indicate humans may be uniquely susceptible to <i>L. stenophrys</i> venom.” (Hardy and Haad, 1998). “80% [mortality] in Costa Rica.” (Campbell and Lamar, 1989). However, I suspect that most bites recorded have been by large (adult) examples, since it is rare to find babies and juveniles in the wild. Since adults have greater venom yield and longer fangs, this may skew statistics. Bites from adult <i>Bothrops</i> are far outnumbered by bites from young and neonate snakes, always more common near human dwellings than their adult counterparts. See text section “Of mice and men. . . .”	Low mortality. ⁶ “Despite apparent potential to produce death (high venom yield; high toxicity in laboratory animals). . . surprisingly low incidence of mortality (1–2%).” (Hardy and Haad, 1998). “7% mortality” (Bolaños, 1982) Based on my own data, assembled from many years interviewing local victims, most terciopelo bites are by <i>neonate or small examples under 1 m long</i> , usually inflicted within agricultural areas, or within range of the victim's own home. Statistics do not reflect “size of snake,” rather only species (although this too is often dubious). Terciopelos collected from agricultural areas do not attain the very large size of those from primary forest situations, i.e., they become conspicuous and are killed. Bites by large (2 m) terciopelos are rather less usual, influencing morbidity statistics. See text section “Of mice and men. . . .”
Venom: quantity versus toxicity	Does not produce much venom: about 333 mg dry weight maximum. ⁶ Quantity does not explain high lethality to humans, which Minton and Minton (1969) estimate at 125–150 mg probable lethal dose for man: one of the “less toxic venoms.” Perhaps “low rodent toxicity” (on which potential toxicity to humans is based) is not a reliable gauge for the effect of this venom in large primates. See text section “Of mice and men. . . .”	Great: over a gram has been recorded from large specimens, which Minton and Minton (1969) estimate at 50–60 mg lethal for man. By any estimate this is one of the world's deadliest vipers. Yet there is a disparity, for human mortality is low. See text section “Of mice and men. . . .”

Table 8. (cont'd)

Characters	Bushmaster (<i>Lachesis</i> sp.)	Terciopelo (<i>Bothrops asper</i>)
Venom: ontogenetic changes	Venom toxicity of adults greater than juveniles. ⁴	Venom toxicity of juveniles greater than adults. ⁴
Size dimorphism	Males 10–20% larger. However, head size is not significantly greater, nor is there an appreciably greater venom yield.	Females larger. ² In terms of mass I find that females can reach up to three times the size of the male. Any terciopelo reaching or exceeding 2 m is without doubt female. In an adult male of equal length to an adult female, the female's head will be double or more the size of the male's, with proportionately larger venom glands. In effect, mortality rate in humans from this species can probably be linked to this sexual dimorphism.
Mimics	Bushmasters may inhabit armadillo (Dasypodidae) burrows. Resident hunters have told me they have grasped by hand (reaching into the burrow) what they thought were the hind-portions of armadillos only to draw out the nonbusiness end of a bushmaster instead! Do the beaded "scales" of armadillos "mimic" bushmasters as an advantage against predation? Are bushmasters commensal with armadillos as local hunters attest (an instance has been recorded in Ripa [1994]), or do they move in only after the burrow-building mammal has abandoned the premises? Perhaps the "hard" body conformation of the bushmaster protects the snake against the sharp claws of the co-habitant mammal; similarly, perhaps the hard shell of the armadillo protects against the bite of the snake.	Campbell and Lamar (1989) list <i>Xenodon rabdocephalus</i> as an ophidian mimic of <i>B. asper</i> .
Recommendation for official protection	None. Official protection of these and most snakes is a symbolic gesture with no practical application. Hinders the work of herpetologists and provides no genuine protection against the overriding pressures of habitat destruction and individual persecution, the latter of which, in regard to snakes, can never be controlled by any law. Protection from the live animal trade is equally worthless, since for every one bushmaster exported to the U.S. probably thousands are killed by normal human persecution. At the very least trade in these snakes saves those particular animal's lives which would otherwise be exterminated whenever encountered. There are few professional snake "catchers" in the tropics, only professional "snake buyers," who use the bounty method to acquire them when they are encountered accidentally by local people. Thus the "pet trade" cannot be deemed causative of a decline of wild populations of these and most snakes, which are inevitably killed regardless of regulations against collecting them.	As for bushmaster. <i>B. asper</i> 's place on Honduras' CITES III list, along with other common venomous snakes, is assuredly ridiculous.
Conclusions	Low adaptation score outside of primary forest situations. High specialization, limited prey-size potential, sensitivity to heat and sun, need for hydoregulation of skin and eggs, small number of young, and large conspicuous adult size, limits these snakes to specific habitat outside of which they cannot survive.	High adaptation score within and outside of primary forest situations. Low specialization, wide range of prey-size and type, tolerance to wide range of temperature, low hydoregulation needs of skin, live birth of young in great number, with an early-reached reproductive size, make these snakes extremely adaptable to most any moist tropical environment within specific elevations.

1. Chiszar et al. (1989).

2. Solórzano and Cerdas (1989).

3. Vial and Jiménez-Porras (1967).

4. Gutiérrez et al. (1980, 1990).

5. I have devised a unique method of extracting venom based on this propensity of bushmasters to "strike-hold first—ask questions later." A dog's rubber play-toy, with a soft, thin, rubber exterior and hollow inside (a "football" shape proved most serviceable), is heated to approx. 40–50°C and offered to hungry bushmasters who seize and strike-hold the item exactly as if it were a prey animal. The venom is expelled into the hollow interior of the

Table 8. (cont'd)

toy and can later be extracted by cutting it open. Because the bushmaster's tendency is to hold on tighter when resistance is offered, one must await the snake's releasing the mock prey item for repositioning to swallow in order to reclaim the venom collecting device (actual swallowing of the object will not occur once the snake's olfactory tells it the item is not food, a more selective process than striking). However, this tenacity is also useful in getting even more venom from the snake, since if resistance is offered the snake will simply bite down harder, injecting more venom. Once strike-hold is taken, one can even massage the glands of the snake (to induce greater venom expulsion) without its releasing its hold on the rubber toy. Using this method I have extracted venom equal to the greatest yields ever recorded for bushmasters (over 300 mg). This method is excellent because it does not injure the snake; the conventional method of "necking" the serpent produces disastrous consequences for the health of the captive (the effects of stress on bushmasters has been discussed, and Ditmars (1910) describes the ill effects of restraining these snakes in order to force-feed them, a process which almost inevitably kills the snake). So treated, the bushmaster will usually begin an inexorable decline as well as reducing the yield of subsequent extractions (note in Bolaños [1972]; venom yield fell from 233 mg to 64 mg after the snakes remained in captivity). Thus, it is probable that toxicity of bushmaster venom may be affected by the *method of extraction*, as is yield; hence, roughly handled snakes may produce less satisfactory venoms on subsequent milkings, and venom extracted from injured or roughly caught snakes may not reflect a true picture of what wild, healthy bushmaster venom really is or does. These contingencies may further amplify the disparity described by Hardy and Haad (1998) of the low laboratory toxicity in these snake vs. very high mortality in persons bitten. The venom collected by conventional methods in the laboratory may be as constitutionally "unhealthy" as the captive.

In regard to this propensity of bushmasters to strike-hold without need of prior prey scent, I suggest that a distinction be made between the forms of strike-hold behavior, which I divide into two kinds: Chemosensorial-Visual Induced Strike-Hold (CVISH), such as can be seen in many viperids, especially the *Bitis* group, as well as many New World pitvipers; and another type, Heat Induced Strike Hold (HISH), as employed by bushmasters. These types may occur in concord but are by no means obligatory to one other. In the former, CVISH, chemical clues qualify the object as prey, and the strike is guided visually to its target. In the case of the bushmaster, chemical clues doubtless play a significant part in locating the hunting site, and determining presence of prey; however heat alone is the final requisite to induce the strike. Chemical clues (and chemosensory searching behavior) may be required only after the fact—that is, after the prey has been subdued or killed—in order to relocate and position the prey for swallowing. Note that the bushmaster will not swallow the rubber ball, but it will strike-hold it, so long as it is warm. (Recall also that the bushmaster will not strike-hold a cold dead rodent, but will strike-hold a warm one. Rarely can bushmasters be induced to eat cold dead prey, and will seldom swallow prey that it has not first struck or strike-held. The feeding episode rarely occurs in the absence of an initial strike sequence.)

One could argue that the smell of prey must be "in the air" or the snake would not launch the strike-hold attack on the rubber ball. This has not been observed to be true; in the majority of cases rodents were not present in the 500 m² area of the facility, nor had rodents been present for many days (to postulate a completely sterile environment where no prey scent existed or *had ever existed* as a better place to conduct such tests is unrealistic, since no such place exists in nature, and even the snake's own body surface could be accused of harboring chemical clues from former feeding sequences). Granted, a greater incidence of strike-holding the rubber ball can be provoked in bushmasters by providing prey-scent in the form of rodents kept caged nearby; what is significant is that prey-scent is not necessary in many cases. (Note: these experiments work only with well-acclimated, feeding bushmasters, usually long-term captives; obviously a snake that cannot be induced to feed at all will not strike-hold the rubber ball, rather it will strike-release it in the typical defense strategy).

HISH in bushmasters has occurred in bites on human beings as well. Mole (1924) tells of a bushmaster bite on the Hon. Albert B. Carr of Trinidad in 1898. From Hardy (1998), "...Carr reached into the burrow of a 'Lappe' (Rodentia: *Agouti paca*) and felt a sharp stab and upon withdrawing his hand saw the head of a large 'Mapepire Z' Ananna' (*L. m. muta*) holding onto his thumb." Evidently, the Hon. Carr was mistaken for prey! This is a typical scenario of the "ask questions later" food-getting strategy of bushmasters. Any warm blooded prey is a candidate to become a food item, and any warm object is a candidate to be strike-held. Your reporter, who has the dubious distinction of being probably "the most bushmaster-bitten person in history," has four times been envenomated by bushmasters, and twice strike-held on account of HISH (a third strike-hold was a defensive-aggressive response; see text section "Of mice and men. . .").

6. Picado T. (1987); Bolaños (1972); Bolaños et al. (1982); Gutiérrez et al. (1980, 1990); Hardy and Haad (1998).

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HerPET-POURRI

by Ellin Beltz

Care in Captivity: Humans in Herp. Society

The recent swirl of letters about the proposed “new” stuff for the *Bulletin* prompts me to point out some very basic facts. If anyone wants to see “new” stuff here (and really none of these ideas are new, many having appeared here over the years in articles, columns and sidebars), they need to consider writing—or at least contributing—something to the *Bulletin*. No one who works on this publication receives recognition (financial or otherwise) for their hours, weeks or years of work. I know some readers may not be aware that this is an entirely volunteer-produced and contributor-driven publication, but I was still struck by the tone of the second Tympanum letter last month—as if the people who write, edit and put out the *Bulletin* were getting paid not to fulfill her expectations. I looked in all my files and couldn’t even find a clipping, note, photo, or anything from that writer ever before. What if all that negative energy had—instead—been focused on writing something that she would like to read? Then we would have had a positive contribution to our publication and saved a lot of hurt feelings all around. I applaud Mike for printing the letter; we need all voices to be heard. But people who say “There’s nothing for me there,” really need to consider their options: (1) Find what you want elsewhere; or (2) Help make what you want a reality. You say there is nothing of interest to you. So write it. Surely that’s where President Kennedy’s head was at when he delivered his famous challenge, “Ask not what your country can do for you—but what you can do for your country.”

On the other hand

My regular contributors sent notes by E- and regular mail asking what happened to the January HerPET-POURRI. Imagine no conspiracies, gentle readers! It was a direct consequence of the blizzard. Apparently my column left my machine just about the time that the power lines dropped. I thought it went; but it didn’t and Mike had to leave for vacation (column or no column) on schedule. We figured it out when the *Bulletin* arrived, a flurry of phone calls resolved what had happened. So your February column was a quick rewrite of the January—and new material and a new year start here. Hopefully there will be something for everyone below.

Mystery solved

Contributor Ray Boldt: “Just a quick note to let you know it was me who had the broken right wrist. It was so physically hard to write with a cast on that sometimes I would lose my train of thought. Anyway the cast was removed . . . and I have been playing catch up ever since.” Ray also sent some lovely pictures of fall sunset at Ryerson Conservation Area. Thanks to Ray for all his help and contributions over the years!

Ribbet and groan

Some of my contributors exceed themselves. . . . This all started when I E-mailed contributor Roger Repp about a desktop juxtaposition. Lying under an issue of *FrogLog* was a beautiful color poster I received from contributor Jim Harding. It features the latter’s photos of frogs and toads of Michigan in

full color. I found the punch line of a joke swirling in my brain; Roger supplied the jokes. Q. Where do frogs bank? A. Under *FrogLogs*. Q. Where do frog researchers save money? A. At the River Bank. Q. Why? A. Cuz they’re saving up for a Ranidae. [Thanks Roger!]

Truck, tractor cap and turtle?

Regular contributor Bill Burnett sent his annual Christmas photo. It shows him by his brand shiny new 4×4 truck. At first, I didn’t see the herp, but looking carefully found the license plate “Tortuga!” Thanks, Bill, for the monthly big envelopes (no origami here, folks)—all decorated with herp stickers and stamps.

Croc Bank finances Andaman project

Romaine Andrews of the Madras Crocodile Bank Trust Centre for Herpetology writes: Greetings and best wishes for the New Year! Enclosed are recent articles . . . which Harry [Andrews] has asked me to forward to you. He is mostly based in the Andaman Islands these days where he has been concentrating efforts over the last two years in getting our conservation, research and education base in South Andaman functional (it’s now complete), besides conducting survey work. One positive outcome of his collaboration with the Andaman and Nicobar Islands Forest Department is the formulation of a management plan for leatherbacks—providing further protection of their nesting beaches and feeding grounds. It is hoped that the recent forthcoming UNDP project in India, will take up the protection of sea turtles on the Indian coast. . . . The Crocodile Bank partially supported most of the sea turtle research activities . . . but we are still struggling to get funding for a comprehensive sea turtle monitoring and study project in the Andamans, that would provide the data required for a complete assessment of the situation in the islands.” You can support the Croc Bank. Contact them at Mamallapuram, Post Bag 4, Tamil Nadu 603 104, India, or fax 91-44-491-0910 & 91.

Continuing threats to India’s sea turtles

Olive ridley sea turtles, which annually nest on the Orissa coast in India, face a new threat: testing and implementation of defensive missiles. This test range is part of the program which has produced long and short range ballistic missiles. Another part of the agency was involved in India’s first nuclear bomb test. Local environmentalists fear that the arrival of the military will further endanger turtle nesting beaches. [Deccan Herald, December 29, 1998] This is the same set of beaches where shrimp trawls have been implicated in the deaths and strandings of over 2,000 sea turtles during ten days of the 1998 season. Trawler owners expressed interests in Turtle Excluding Devices (TEDs) when they were demonstrated to them by American wildlife officials. However, no one in India is making TEDs and it hasn’t occurred to international wildlife groups to just send TEDs or instructions on how to make a TED, and so the turtles continue dying. [Sunday, Vol. 25, #7, February 1998, both from Romaine and Harry Andrews] Meanwhile, the U.S. lost its restrictive import clause

banning imports of non-TED shrimp. The World Trade Organization in Geneva ruled that “the restrictions were an illegal attempt to impose U.S. standards on other countries.” [*New Orleans Times-Picayune*, October 13, 1998, from Ernie Liner]

Watching exceeds killing

A recent press release by the U.S. Fish and Wildlife Service shows that the number of people who watch wildlife vastly exceeds the number of people who hunt, even in Texas! Expenditures in millions for wildlife watching for the top five states were: California \$2.4, New Jersey \$1.8, Florida \$1.6, Washington \$1.6 and Wisconsin \$1.5. The number of people resident in the state in which they watch wildlife, also in millions: California 5.9, Texas 3.5, Pennsylvania 3.4, New York 3.1 and Illinois 3.1. By contrast, the states with the most number of ammunition purchases were Texas 636,000, Michigan 211,000, Wisconsin 166,000, Missouri 162,000 and Ohio 155,000. You can get the whole release by calling Eric Eckl at (202) 208-5634.

How to protect a species by killing individuals

“Federally protected gopher tortoises were plowed under by bulldozers at the building sites for new elementary schools in Clermont and Astatula because officials said they didn’t have the time to move them. . . . The Lake County school district faces an estimated \$75,000 in fines from the Florida Game and Fresh Water Fish Commission because [the district] did not get the necessary permits to either move or kill the tortoises.” The director of facilities for the school district said, “All of those construction dollars sitting there idle for that time exceeded the possible fine.” He also “acknowledged that school officials made a conscious decision not to get the needed permits because they were in a hurry to get the two schools finished by next July. . . . [A member of the school board] said, ‘We are teaching our kids to violate the law if it is convenient.’” The fines will go to a fund to purchase land for the rapidly disappearing tortoises. [*The Lake Sentinel*, October 27, 1998] Local pundit Ramsey Campbell suggested that the school superintendent be forced to take a class on why killing gopher tortoises is wrong and then be “forced to write ‘I will not kill gopher tortoises’ on the blackboard a couple gazillion times.” [same paper, November 4, 1998, both from Bill Burnett]

Big snake stories close to home

Writing this column for more than 10 years now has filled my files with many “big snake found slithering loose” stories, but few have been from around here until now.

- Midsummer there was a report of a “huge” snake—wrong name, right photo—still getting copies of that story as it bounces around the U.S. [Ray Boldt, Claus Sutor and ??? no name on clipping]
- Police apprehended a 12-foot-long python that was found, not slithering around Schaumburg’s giant mall, but sunning instead, on a grassy embankment along Meacham Road. It was noosed and put in a large cat cage and transported to a vet for a checkup. The snake appears to be in good health. Whether it escaped on its own or was released for being “too

big,” we may never know. [October 14, 1998, *Chicago Tribune*, from Claus Sutor]

- Now in 1999 we hear of a 14-foot-long, 81-pound Burmese removed from its seven-year home in south suburban Thornton by police and animal control officials. The animal was taken to the clinic of Mike Miller, DVM (contributor to the CHS “Care-in-Captivity” brochure and many other CHS projects over the years) where the python received a check-up and an overnight stay. The next day, Brookfield Zoo offered a temporary home for the snake. According to Mike, the owner hopes to regain custody, although state law prohibits keeping of a potentially life-threatening snake of more than 6 feet as a house pet. [*Chicago Tribune*, January 16, 1999, from Ray Boldt]

Other local tales

- First Chicago Bank had a cute frog picture on the cover of its home equity brochure. The caption reads “Use your pad for a major purchase.”
- The 61-year-old Lockport, Illinois, man arrested last September by Illinois Department of Natural Resources officers when they discovered hundreds of turtles (including 158 baby turtles) in his home and yard and more than 100 pounds of turtle meat in the home, pleaded guilty and was ordered to pay fines and court costs in excess of \$1,000. Had his case gone to trial, he might have been jailed and fined far more than a grand. [*Chicago Tribune*, November 21, 1998, from Claus Sutor]

Another big snake heist

Thieves stole 68 snakes for a private home in Mesa, Arizona—in broad daylight! Their owner is offering a \$10,000 reward towards recovery of his boa constrictors and ball pythons. A recent U.S. Fish and Wildlife raid seized allegedly smuggled monitor lizards from the same home. Although the owner was not indicted in the operation, he feels that publicity about the case may have led to the thefts. [*Arizona Republic*, October 31, 1998, from Tom Taylor]

Ex-dealer admits smuggling

Tom Crutchfield entered guilty pleas to one count of conspiracy and six of smuggling, aiding and abetting the importation and sale of rare reptiles during a hearing in Orlando, Florida. He owned of Tom Crutchfield’s Reptile Enterprises near Bushnell, Florida, before fleeing the U.S. and fighting extradition from Central America. At the time of his flight, he was on federal probation for a 1995 conviction for smuggling Fiji Island iguanas. More time may be added for leaving the country without permission during probation. Three other charges were dropped by prosecutors in exchange for the guilty pleas. Sentencing in the case has been set for April 16. Crutchfield was the 18th person charged in a single probe stemming from a customs bust at Orlando International Airport in August 1996. Still being sought are Mrs. Tom (Penny) Crutchfield, and two German nationals. [*Orlando Sentinel*, January 12, 1999, from Bill Burnett]

Time to buy a water filter

A wave of recent alligator deaths and sea turtle tumors may be the result of algal overgrowth. Algae, is a natural thing, but too much of anything can prove bad for a system, so the increase in algae due to increasing fertilizer runoff, is of concern. The study focused on the deaths of about 50 alligators at Lake Griffen in Lake County, Florida. Public health officials are concerned that blue-green algae may cause more than taste and odor problems in public water supplies. [*Orlando Sentinel*, October 19, 1998, from Bill Burnett]

Too much of a good thing?

Residents of Desha County, Arkansas, are concerned because a 7-foot alligator was recently found in their area and because a child was bitten by a gator in the next county south. Alligators were imported years ago to help with the “beaver problem,” but both beaver and gator still exist on the county’s 150 miles of riverbanks. Animal control officers pointed out that while people are afraid that they still have more reports of trouble with bears than gators. [*Arkansas Democrat-Gazette*, October 24, 1998, from Bill Burnett]

A sad zoo loss

The white alligator “Paleface,” a star attraction for a decade at the New Orleans Aquarium for the Americas died after choking on a coin which was tossed into his habitat by a visitor. The animal was found in 1987 along with his 17 brothers and sisters. While not technically albinos, they have white skin and bluish/gray eyes, which makes their mutation leucistic, an even rarer form of whiteness in alligators. [*Houma, Louisiana Courier*, December 26, 1998, from Ernie Liner]

Tai-cane-toad-o?

Cane toads, originally native only to South America, are the first species to provide evidence of lopsidedness in visual stimuli processing in amphibians, according to two researchers in Australia. They found that cane toads are more likely to throw a punch at another cane toad if the second one hops to the left side than to the right. Curiously, prey are zapped more often on the right than on the left. [*Science News*, November 7, 1998, from Mark Witwer]

Time to get shot full of Lyme

Gary Casper writes: “For those of you field workers at risk from Lyme disease, this may interest you. The Minneapolis *Star Tribune* published an article today on the new Lyme vaccine now available and covered by most insurance companies. See <<http://www2.startribune.com/cgi-bin/stOnLine/article?thisSlug=lyme05>>”

Special thanks to:

- Lori King-Nava, Ray Boldt and Claus Sutor for the “No newts is bad news for tour” article which briefly quoted my husband, Ken Mierzwa, as “an expert on newts.” We newt that.
- Julian Bentley for dropping in on O’Hare airport for a few brief minutes to catch up on our home/family/herp news. It was great to see Julian again, even if for such a short time!

For those of you who know him, he’s been posted to Australia by his employer (from the U.K.). Since Julian is a salamander expert, this must be close to torture. Perhaps he’ll develop an interest in venomous snakes or cane toads or something instead!

- My E-mail correspondents for making new stuff magically appear in my mailbox which I really appreciate, but cannot (due to copyright) use unless I receive an original of the article, too.
- Bill Burnett’s mom for being our best Florida correspondent!
- Bill Burnett for contributing material to the CHS for the *Newsletter* long before I started doing this column!
- Ernie Liner for a decade of super contributing from Louisiana. I don’t think a single clipping escapes his scissors from any of five newspapers!
- Mark Witwer for covering *Science* and *Science News* for many years!
- P. L. Beltz for clipping before, during and after his cancer treatments.
- Kim and Wes von Papineau, two fantastic newts-gatherers, for going electronic with their massive, global contributions! Even though it took several tries to iron out E-bugs, I think we’ll save two trees this year.
- The government of Canada for its continuing contributions to herpetology.
- Don Wheeler for drawing “The Adventures of Spot” for longer than most of us have been members! How about a collected works of Wheeler for our 30th Anniversary?
- To Gary Kostka and Debi Hatchett for writing about CHS meetings. That is far and away my favorite written section in each *Bulletin*, followed closely by Board Meeting News, classified ads and upcoming meeting announcements.
- To John Murphy and Mike Dloogatch for everything they’ve done and everything they will do to put out the CHS *Bulletin*.
- The regular CHS volunteers and board members without whom we’d have no membership, no meetings and no *Bulletin*.
- To everyone who has ever contributed to this column, a big heartfelt thanks.

We can’t write without you. Please contribute news and magazine articles, letters, photos, news about herps and your herps (and you!). Previously published articles need to have the date/publication slug attached to each page. Whole sheets of newspaper can be mailed for a first class stamp—so save your scissors and just send the page! Be sure your name is on each piece. I credit every contributor, but we have a lead time, so it may take a while for you to see your name in the *Bulletin*. Mail contributions to: Ellin Beltz, 1647 N. Clybourn Avenue, Chicago, IL 60614-5507. E-mail (text only) to <ebeltz@ripco.com>.

Letter from the President

Dear Members:

Spring is in the air and the snow has finally decided to give us a break. What a winter we've had. Luckily we didn't encounter any serious problems when it came to our herps. At least in my house, the power held on in spite of bad weather and everyone was able to keep hot and happy, and for my desert lizards, this is a good thing!

This February, I underwent a major hip operation that has kept me away from the society all month. I am happy to report all is well with me and I am recovering quite nicely. A heartfelt thanks to everyone who sent cards, flowers and made phone calls to help my recovery along. I look forward to the March meeting to see everyone again.

In spite of my absence, I have been busy doing CHS stuff at home, planning more things for the coming year. Things like the annual picnic and the zoo field trip.

I have secured a picnic permit for Sunday, August 22, 1999. It will be at the Catherine Chevalier Woods in Chicago (near O'Hare) as it was last year. I doubt we will encounter the difficulties we did last year as we were up against another picnic nearby called "Freaknic," which made headlines as a traffic and local nightmare for residents of the nearby neighborhoods. Several members got lost trying to find our picnic grove because of traffic being re-routed. Things should be a lot smoother this year. There will be a picnic potluck sign-up sheet at the membership table for those wishing to attend. A

dish to share would be appreciated, so sign up for your contribution at the general meeting, so that we don't have 20 tubs of potato salad! A games committee needs to be organized as well. The society will again provide soft drinks and paper goods and a community BBQ grill, but you can always bring your own grills and provisions. This is great family fun and a good time to be had by all. See or call me for further details.

I have been in contact with the Louisville (Kentucky) Zoo and it looks like that's where we'll be trekking to this summer. The date will be Saturday, June 19. Please keep this date in mind as there is limited seating and reservations are required. These field trips are always a treat as we go behind the scenes and meet with the head zookeepers and see what's new and exciting with the herps! Last year was a real "hoot" as the Chicago Bulls were playing their final championship game and we had to hear play by play details via a hand held transistor radio. Everyone was a good sport in spite of the game being played on the same day as our field trip. In my humble opinion, I truly doubt that will interfere with this year's agenda.

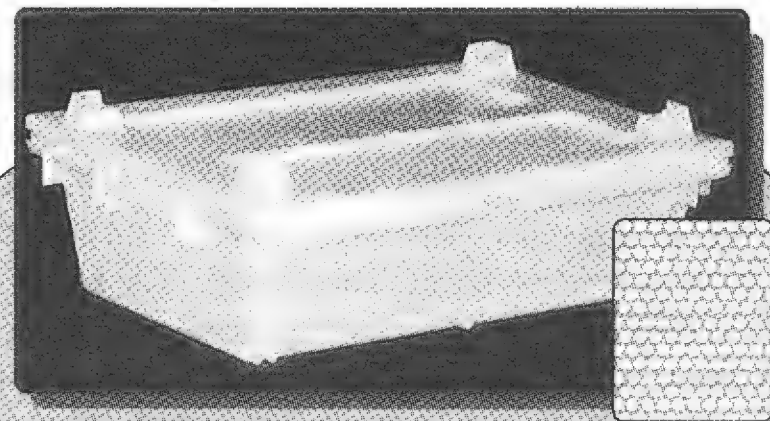
To those of you who are breeding animals this spring, I wish you well, as this is a particularly nerve wracking time of year for me. Having some years behind me now as far as experience goes, I'm not as neurotic as I used to be, but I still empathize with those new to breeding and even those not new to it! Next month we can talk about our experiences and outcomes! Till then, keep your herps happy and healthy!

Sincerely, Audrey Vanderlinden

Health Food for your herps!



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Media Notes

compiled by Lisa Koester

Have you seen an interesting article, photo or website that you'd like to share? Please send your sightings to Lisa Koester, 6121 N. Fairfield Avenue, Chicago, IL 60659, (773) 508-0034, or E-mail: <rlkoester1@earthlink.net>. Here are some. . . . Have fun!

Magazines

Lizards:

Scientific American, March 1999. An excellent, long (pp. 84-91) article by Claudio Ciofi entitled "**The Komodo Dragon**," provides good background information on the lizard, as well as the very latest on conservation and on research being done with these monitors. In the "Further Reading" section at the end of the article is a mention that "A lecture by Walter Auffenberg is available (in Real Audio) at www.si.edu/natzoo/hilights/lectures.htm on the World Wide Web."

Snakes:

Scientific American, March 1999. On page 49 is a paragraph describing the drug captopril (used to relieve high blood pressure). It mentions that the drug was developed following research on the venom of a **Brazilian pit viper** (a picture of which is included).

Ranger Rick, March 1999 (p. 2). Close-up photo of a **vine snake**.

Turtles / Tortoises:

Scientific American, March 1999, pp. 21 & 24. An article in the "In Brief" section (including a photo) deals with the conservation of **Galapagos tortoises**. It discusses the use of DNA analysis to identify the various subspecies.

Wildlife Conservation (the magazine of the Wildlife Conservation Society, i.e., the Bronx Zoo), April 1999. An article called "Townsend's Tortoises," written by Downs Matthews, describes an expedition to the Galapagos in 1928 led by Charles Townsend, then director of the New York Zoological Society's New York Aquarium. The expedition brought back 180 young **Galapagos tortoises** from the island of Isabela. The article is on pages 32-35 but the first two pages consist of a photograph of the smallest of the 180 tortoises perched on the head of the largest.

Frogs:

Sierra, March/April 1999, p. 16
What's Wrong with the Frogs?

International Wildlife, March/April 1999, p. 9
Vermont Study Finds Hot Spots of Frog Deformities

Scientific American, March 1999. On page 30 is a photograph captioned "Ignoble end for a **Bufo marinus**." It shows a toad that has been tanned, with a zipper down its belly, for use as a change purse.

Ranger Rick, March 1999, p. 18. Frog Force: The amphibian dilemma explained re: habitat destruction, pollution etc. (for the youngest herpetologists among us).
w/ URLS

Ranger Rick, March 1999, p. 18. Frog Egg Hunt: advocating observation, not collection. Geared for the young.

Ranger Rick, March 1999, p. 2. Article on noses features close-ups of **barking treefrog**, **shovel-headed treefrog**.

Crocodylians:

Ranger Rick, March 1999. **Gavial**: 2-page head close-up.

International Wildlife, March/April 1999, p. 9. **Alligator** illustration.

People:

International Wildlife, March/April 1999. An article on the endangered St. Lucia parrot includes (p. 43) an interesting sidebar entitled "Donald Anthony: Lizard Champion." Wildlife officer Anthony has been relocating St. Lucia whiptail lizards to an islet that has been cleared of mongooses.

Internet Sites

International Herp Websites Directory (including Medical Herpetology)
<<http://www.xmission.com/~gastown/herpmed/>>

Herpetological Contents (latest herp articles)
<<http://www.herplit.com/contents>>

Common and Scientific Names for North American Herps
<<http://eagle.cc.ukans.edu/~cnaar/>>

North American Reporting Center for Amphibian Malformations (NARCAM) (includes ID guide for species, maps of states with deformities)
<<http://www.npwrc.usgs.gov/narcam/>>

Reptile and Amphibian Conservation site
<<http://www.flmnh.ufl.edu/arc/>>

Turtles of the World (John Iverson's checklist with maps, references etc.)
<<http://bufo.geo.orst.edu/turtle/>>

Crocodylians, Tuatara and Turtle Species of World checklist
<<http://www.flmnh.ufl.edu/natsci/herpetology/turtcroclis/>>

Aquatic Snake Web Page
<http://www.flmnh.org/candr/zoology/zoo_sites/snakes/default.htm>

Ranger Rick
<<http://nwf.org/nwf/rrick/>>

Contributions by Mike Dloogatch, James N. Stuart
and Harold K. Voris.

More Thoughts on ReptileFest '99

by Gary Kostka

Well, here it is the end of March and there's just a little over one month remaining until the herp happening of the millennium — ReptileFest '99. Hopefully you've decided to take part in this monumental event and have busied yourself over the past month dreaming up new and exciting ways to display your herps.

Remember, the two principle goals of ReptileFest are entertainment and education, so try to design your exhibits with those things in mind. Your leopard gecko will be considerably more fascinating to 'Fest attendees if he's seen prowling about in a desert landscaped vivarium rather than frozen in fear in an empty styrene shoebox. You might even go one step further by placing the vivarium within a larger, darkened enclosure and lighting it with a red or blue bulb. This would create a dramatic, eye-catching effect as well as providing viewers with a glimpse into the leopard gecko's nocturnal lifestyle.

Graphic materials relevant to your display will also help to ensure that it will be remembered long after the 'Fest has ended. Perhaps you'll be exhibiting a corn snake at ReptileFest '99. It's safe to assume that most visitors to your exhibit will be unaware of the variety of multi-hued corn snakes established through captive breeding. Why not consider making a professional-looking poster featuring photos and descriptions of the various color morphs of the species for inclusion in your display? This type of visual information will go a long way toward helping visitors understand and appreciate the extent to which the pursuit of herpetoculture has evolved.

Books or magazines featuring information such as range maps and natural history accounts pertinent to the herps in your exhibit will be eagerly perused by a public keen to learn more about these enigmatic creatures. These resources, coupled with your own cogent comments are bound to give 'Fest visitors a greater appreciation of these animals and the important roles they play in the ecology of our planet. Bear in mind that any materials placed on display will be handled by a great many people, so take appropriate precautions to protect them. Treasured volumes and rare or irreplaceable materials are probably best left at home.

Perhaps the most memorable experience for many visitors to ReptileFest will be the opportunity to interact with animals with which they've had little or no prior experience. It's extremely rewarding to see someone overcome their trepidation as they tentatively extend a hand to touch, or perhaps even hold an animal which they may previously have considered loathsome or frightening. If you do choose to share your animals with the public in this fashion, please be sure to do so only with those animals which you know to be nonaggressive. If there's even the slightest doubt in your mind as to the trustworthiness of an animal, don't even consider removing it from its enclosure. It would only take one negative incident, no matter how minor, to seriously undermine the public's trust in the CHS and its ability to safely conduct events such as ReptileFest. I'm confident that all exhibitors will understand

the importance of this issue and conduct themselves accordingly.

All of the nifty displays and friendly critters out and about at ReptileFest '99 won't mean a thing unless we draw a crowd, and we won't draw a crowd unless we promote the event. **PROMOTION!** This is the one aspect of ReptileFest '99 in which every CHS member in the Midwest could . . . nay, should become involved. ReptileFest is the CHS's banner event of the year and thus merits our most diligent effort to spread the word far and wide to all those who might have an interest in attending.

ReptileFest '99 fliers are available for distribution and may be picked up at the March general meeting or by contacting either Lori King at (773) 477-3645 or Gary Fogel at (773) 935-6938. So whether you plan to participate in 'Fest '99 or not, do the CHS a great service, grab a stack of ReptileFest fliers and paper your town with them. Don't limit yourselves to the obvious locations such as libraries, schools, nature centers and pet stores either. Place them at the vet's office, the grocery store, the barber shop, the dentist's office and at your own place of business. In fact, place them anywhere that people will be likely to notice them. It won't take much time, and your efforts will be rewarded with a heightened sense of self-esteem gained from the knowledge that you've done something beneficial for the CHS. Please remember to secure permission before you post or set out any fliers.

Word-of-mouth is another effective promotional technique which can be pressed into service in the event that you find yourself sans fliers. Don't be shy. Tell everyone you know about this marvelous opportunity to experience these wonderful creatures firsthand. Make absolutely certain that you've got all the details concerning dates, times and location of the 'Fest straight in your own mind before passing them along though. Remember. When applying the verbal approach, words like "magnificent," "unforgettable," "spellbinding" and "greatest show of its kind known to man" will help pique a listener's interest.

If you think your town's local paper might be interested in listing ReptileFest '99 in their Upcoming Events section, have them contact either Lori or Gary at the above-listed numbers and they'll be more than happy to fill them in on all of the particulars. In fact, any mention of ReptileFest '99 in the media, whether print or broadcast, should first be cleared through either of the 'Fest coordinators. Trust me, they won't mind the extra work, and besides, if you're influential enough to have access to the media then you ought to be on the ReptileFest Committee anyway!

As a member of the ReptileFest '99 Planning Committee, I'm excited about the potential for this year's show to be the most spectacular and successful ever. A number of new features have been added including a magnificent collection of ancient chelonian fossils and the Dinorama exhibit which absolutely defies description! It's already beginning to look as if we'll surpass last year's level of vendor participation

and judging from the pre-'Fest buzz that's building among the CHS membership, we're confident that we can establish a new record for exhibitor participation as well. I urge all of you who plan to exhibit animals at ReptileFest '99 to get your applications in to Ron Humbert as quickly as possible, either by mail (his address is listed on the form) or by handing it

directly to him at the March general meeting.

We need to combine our efforts and build on tradition by making this year's 'Fest the greatest ever. If we all get involved and pull together, the CHS can make herpetological history. Shout it across the land! ReptileFest '99 is coming! It's hip, it's herps and it's happening May 1-2.

Unofficial Minutes of the CHS Board Meeting, February 12, 1999

The meeting was called to order at 7:45 P.M. Board members Gino Martinez, Jennie Picciola and Audrey Vanderlinden were absent.

Officers' and Committee Reports

The minutes of the January Board of Directors meeting were read, corrected and accepted.

The Treasurer's report was read and accepted.

ReptileFest: Lori King-Nava reported that the contract with Northeastern has been signed and everything is on schedule. The next ReptileFest committee meeting is February 20, at 4:00 P.M., in Mike's office. The advertisement is published in *Reptiles* magazine. Don Wheeler's tattoo parlor will again be at this year's ReptileFest.

Adoptions: Rich Crowley is replacing Tonya Maris this year as chair of the adoptions committee. We thank Tonya for a fine job.

Grants Committee: Lori King-Nava and Greg Brim volunteered to be included on the Grants committee. Drs. Bruederle and DeLaNavarre have also expressed interest in this committee.

Old Business

The Salamander Safari will be on March 27 at Camp Sagawau. There will be a slightly different format than the previous ones. There will be an amphibian display and presentation which will be followed by guided walks if anyone would like to venture out to observe salamanders.

New Business

Jack Schoenfelder pointed out that the lack of book sales has affected membership. He suggested that merchandise be available to CHS members at the general meetings, such as items from his Reptiques shop, and perhaps dry goods but no live animals. He stated that the CHS would receive some financial compensation, but the society would not be responsible for any sales tax. Other factors considered were receiving permission from the museum, the society's nonprofit status, and holding a three-month trial period for vendors in order to establish rules and regulations for these activities. A motion was introduced which would allow Jack Schoenfelder to sell merchandise at the February general meeting to allow the Board of Directors to assess the effect of this on the membership and the meeting. The motion was seconded and the

vote was unanimous in favor.

Mike Dloogatch informed the board that the director of the Chicago Academy of Sciences has resigned and the CHS may need to develop a new liaison at this institution.

Round Table

Jenny Vollman announced that she will continue to order Vitalites for sale at the general meetings. She would also like to see books which have been written by guest speakers arrive early.

Lori King-Nava said that she would like to get biographical information about the speakers and try to get this into the newspapers for more publicity.

Steve Spitzer suggested that the CHS phone line should have shorter messages and that maybe the board members could handle these calls on a rotating basis.

Jack Schoenfelder asked about getting a Symposium committee together for the 2001 Midwest Herpetological Symposium.

Greg Brim put forth a request for E-mail addresses.

On behalf of the entire board, Mike Dloogatch wished Audrey well after her surgery.

The meeting adjourned at 9:00 P.M.

Respectfully submitted by the Recording Secretary
Karen Bielski

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For sale: from **The Mouse Factory**, producing superior quality, frozen feeder mice and rats. New prices, new sizes, and now rats! Our mice and rats are vacuum-packed to greatly extend freezer life by reducing freezer burning and preserving vitamin and nutrient content. We feed our colony a nutritionally balanced diet of rodent chow, formulated especially for us, and four types of natural whole grains and seeds. Mice: pinkies, \$.25; fuzzies, \$.30; hoppers, \$.35; weanling, \$.40; adult, \$.45. Rats: starting with pinks at \$.40 each, to XL at \$1.80 each. Discount prices available. We accept Visa, MC, Discover or money orders. P.O. Box 85, Alpine TX 79831. Call us toll-free at (800) 720-0076 or visit our web site <www.themousefactory.com>.

For sale: from Bayou Rodents, excellent quality feeder mice and rats. Every size available. Pinks starting at \$20/100. Orders are shipped by overnight service Monday thru Thursday. We accept Visa, MasterCard and Discover. For more info, contact Rhonda or Peggy, (800) 722-6102.

For sale: **high quality frozen feeders**. Over a decade of production and supply. Seven sizes of mice available: small newborn pinks up to jumbo adults. Prices start at \$25 per 100. Feeders are separate in the resealable bag, not frozen together. Low shipping rates. Free price list. Kelly Haller, 4236 SE 25th Street, Topeka KS 66605, (913) 234-3358 evenings and weekends.

For sale: Herp bags—colors vary, translucent ripcord nylon, super lightweight, extremely durable construction with hot corners sewn in, double seamed. Custom sizes made upon request. Sizes: 46" × 14", \$7 each; 24" × 12", \$6 each; 24" × 6", \$5 each. Shipping fees, \$1 for first bag, \$.30 each additional bag. Nicole Lechowicz, 2511 S. Illinois Avenue, #104, Carbondale IL 62901, (618) 457-2783.

For sale: collection of *Vivarium* magazine, 40 issues in excellent condition, vol. 2, no. 5, through vol. 9, no. 3, some out of print, \$200 plus shipping and handling. Mike Kreger, (301) 504-5563 days, (301) 725-7433 evenings. [MD]

For sale: Australian herp books. *Australia's Reptiles* by Wilson and Knowles, 1988, 447 pp., 847 color photos, as new cond., \$110; *Graeme Gow's Complete Guide to Australian Snakes*, 1989 (1993), 171 pp., numerous color photos, \$50; *Dangerous Snakes of Australia* by Eric Worrell, 1961, 68 pp., b & w photos, plastic covers, top of spine peeling, \$25; *Dangerous Snakes of Western Australia* by G. M. Storr, 1977 (2nd ed.), 24 pp., b & w photos, softbound, \$12; *Encounters with Australian Animals* by Harry Frauca, 1963, 152 pp., many b & w photos, author's personal experiences including 35 pp. on reptiles, \$35; *The Puffin Book of Australian Reptiles* by Helen Hunt, 1983, 73 pp., 24 color and many b & w photos, softbound, \$15; *Poisonous Australian Animals* by Dr. Struan Sutherland, 1983, 48 pp., color photos, includes info on snakebite treatment, plastic covers, \$12. Last two books are children's books. All books in very good to excellent condition unless otherwise indicated. Orders over \$25 include postage, otherwise \$2.50. William R. Turner, 7395 S. Downing Circle W., Littleton CO 80122, (303) 795-5128 after 6 P.M. local time and weekends.

For sale: **Reptile terrarium/aquarium**, \$150 or best offer. Oak aquarium stand with cabinets underneath. Will hold 2 adult iguanas. Handmade, original cost, \$900. Vita-lite and heat lamps built in, heat rocks included, able to hold a 180–200 gallon aquarium on top. Dimensions: L-6 ft 2 in., W-2ft 1 in., H-4ft 1 in. Call Judy at (630) 724-0786 if interested.

For sale: Neodesha reptile cages—4' with divider, elongated vents, litter dam, Flex-watt heat and 2' lights, \$165; 2' with glass door, elongated vents, \$35. All in excellent condition. (708) 361-5835.

For sale: adult pair of Australian redbelly turtles (*Emydura subglobosa*), \$100/pair. Wayne, (847) 398-3733.

For sale: adult blue-tongue skink, \$50; male boa constrictor, \$100. Marc, (815) 293-0989.

For sale: Due in June: Third generation Bob Sears strain Hog Island boas, selectively bred for light, clean backgrounds with muted saddles and bright orange tails, none better at any price, \$125; Brazilian rainbow boas from bright, iridescent orange adults, \$125; jungle carpet pythons from 4½-foot bright gold and black adults, \$200. Mark Wendling, (319) 857-4787, E-mail: <kwendling@msn.com>

For sale: three male and four female breeder select emerald tree boas, captive bred and raised by me, 2½ to 4½ years old, were held back to be part of my breeding colony, all excellent healthy specimens, \$1000–1400 each; yearling Amazon tree boas, \$150 each; yearling bar-neck amethystine pythons, tame and beautiful, really neat animals, \$250/pair; one male and two female '95 Borneo bloods, exceptional specimens, \$175 each. Paul Edwards, (843) 766-2416 anytime. [SC]

For sale: two male and one female c.b. '98 Stuart's milks, \$200/trio. No list this year, watch this space. Henry Cohen, 24 St. Johns Place, Buffalo NY 14201, (716) 881-6724.

For sale: Great snakes, great service. Send SASE for list. Applegate, P.O. Box 338, Campo CA 91906, (619) 478-5123. E-mail: <applesnake@juno.com>. Website: <www.applegatereptiles.com> Thank you, call me.

For sale: **Adults:** male het ghost, \$60; black king, \$55; male *thayeri* (milksnake phase), \$100; pair of ball pythons, \$175/pair; Indonesian bluetongue, \$55; *Rhacodactylus auriculatus*, c.b. '98, \$150; *Phelsuma madagascariensis grandis*, c.b. '98, \$20. Flexwatt heat tape, \$2.50/ft, \$5 each connection. Steve Bostwick (515) 274-4580, E-mail <liasis@juno.com>. [IA]

For sale: single carpet pythons, c.b. 7/98, parents high-yellow and solid jet black, \$200; 50/50 Cal. kings, \$50; female Arizona mountain kingsnake, 2-year-old, outstanding color pattern, \$175. Mark Petros, Strictly Serpents, (847) 854-3259.

Tours: Adventure tours to Madagascar! Join **Bill Love** seeing and photographing fauna and flora, heavily herp-biased, across the world's least known mini-continent. Maximum fun & photo ops assured on every trip. Contact him at: BLUE CHAMELEON VENTURES, P.O. Box 643, Alva FL 33920. TEL: (941) 728-2390, FAX: (941) 728-3276, E-MAIL: <blove@cyberstreet.com>.

Tours: **Road-riding in Costa Rica!** Treat yourself to the trip of a lifetime! Learn about tropical herps, find them, photograph them, see where they live. **Greentracks, Inc.**, offers the best herpetological tours led by internationally acclaimed herpetologists and herpetoculturists. See the Amazon, visit cloud forests, experience the world's greatest rainforest, super sunsets and good company. Call (800) 9-MONKEY.

Wanted: unusual/aberrant garter snakes and unusual/aberrant/large rubber boas. Scott, (919) 934-0110, EST. [NC]

Line ads in this publication are run free for CHS members — \$2 per line for nonmembers. Any ad may be refused at the discretion of the Editor. Submit ads to: Michael Dloogatch, 6048 N. Lawndale Avenue, Chicago IL 60659, (773) 588-0728 evening telephone, (312) 782-2868 fax, E-mail <MADadder0@aol.com>.

UPCOMING MEETINGS

The next meeting of the Chicago Herpetological Society will be held at 7:30 P.M., Wednesday, March 31, at the Field Museum of Natural History, Roosevelt Road at Lake Shore Drive, in Chicago. Dr. Gordon H. Rodda of the USGS Biological Resources Division, Fort Collins CO, will speak on: "Tropical Islands and a Biodiversity Serial Killer: The Brown Treesnake on Guam and Other Stories." Dr. Rodda is the primary editor of the recently published *Problem Snake Management: The Habu and the Brown Treesnake*.

The program April 30 will be "The Herpetofauna of Thailand and Laos." The speakers will be Tanya Chan'ard, Brian Stuart and John Murphy, all of whom have been conducting research in Southeast Asia for the Field Museum.

We are required to use the entrance on the west side of the museum. **We are allowed to use the free parking lot to the west of the museum. Entrance to this lot is from McFetridge Drive, the wide street just to the south, between the museum and Soldier Field.** Public transportation is an option: the Roosevelt Road (12th Street) bus goes directly to the museum, thus providing a connection with the el and subway. This bus service runs until 11 P.M.

The Chicago Turtle Club

The Chicago Turtle Club will meet on Sunday, March 14 and April 25, 1:00 – 3:30/4:00 P.M., at the North Park Village Nature Center, 5801 N. Pulaski, in Chicago. Meetings are informal. Questions, children and animals are welcome. Parking is free and there is no admission. April is our Touch a Turtle and Tickle a Tortoise Day. Set-up begins at noon, public is admitted at 1:00, show ends at 3:30. For more information call Lisa, (773) 508-0034 or visit the CTC web site: <<http://www.geocities.com/~chicagoturtle>>.

UPCOMING CHS EVENTS

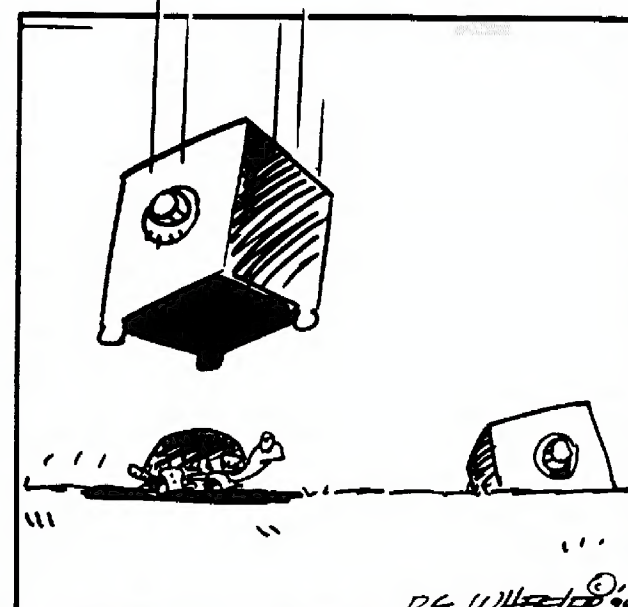
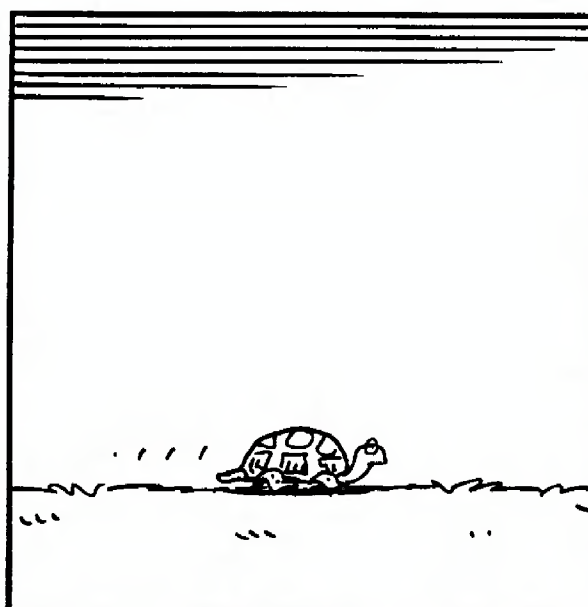
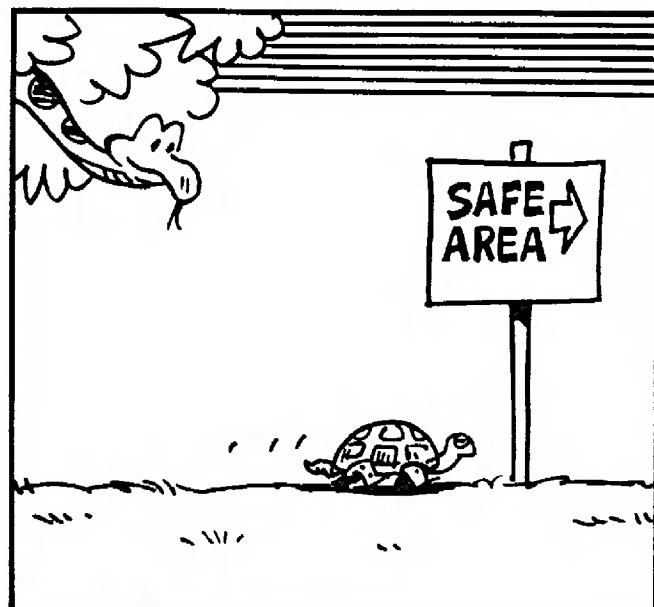
Salamander Safari

March 27, 9:00 A.M.–1:00 P.M., Camp Sagawau, 12545 W. 111th street (route 83 and 111th Street), Lemont, Illinois. Everyone is invited to bring and display an their amphibians in nicely set-up terrariums. This is a great photo opportunity and chance to discuss an often times overlooked segment of our natural history! There will be a slide presentation and discussion. Small parties will allowed onto the preserve to observe the wildlife; weather and staff permitting. Removing plants and animals from the preserve is strictly prohibited. Hope to see you there. Contact Ron Humbert at (630) 620-7377 if you have any questions.

Louisville Zoo Trip

It's that time of year again! Sign up for annual CHS zoo trip — this year to the Louisville Zoo on Saturday, June 19. This is a great opportunity to enjoy a day at the zoo with fellow CHS members as well as members of the Louisville Herpetological Society, who will be joining us this year. Meet new herp friends as we go behind the scenes with the head keepers of the reptile exhibits and learn about the workings of a world class zoo. The newest additions to the zoo's herp collection are a pair of young Komodo dragons! The bus will depart at 6:00 A.M. from the vicinity of the North Park Village Nature Center at Pulaski and Bryn Mawr. Parking will be along the south side of Bryn Mawr Avenue, same as last year. We will arrive at the zoo around 11:00 A.M. and depart at 5:00 P.M. We will make a fast food dinner stop on the way home. Snacks and sack lunches are encouraged and you may also make food purchases at the zoo. The cost is \$46.50 per participant. This covers round-trip bus fare on an air-conditioned luxury motorcoach complete with VCRs, and admission to the zoo. Seating is limited, so sign up early! Paid reservations are required. Make checks payable to the CHS. See Audrey Vanderlinden for reservations and further details. Call (773) 836-2477 or E-mail at <uromastica@aol.com>.

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